Relationships of the laticaudine sea snakes (Serpentes: Elapidae: Laticaudinae)

C. J. McCarthy
Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

Introduction

The genus *Laticauda* is considered by some workers to constitute the most primitive group of the sea snake family Hydrophiidae. However, others consider that *Laticauda* (Laticaudinae) and the true sea snakes (Hydrophiinae) are more likely to have had separate origins within the front-fanged proteroglyphous snakes (family Elapidae).

The paper considers morphological evidence for the relationships of laticaudines at a number of levels. Firstly, variation within the currently recognized species of *Laticauda* is discussed and clinal variation within the wide-ranging forms *L. laticaudata, L. colubrina*, and *L. semifasciata/schistorhynchus* is reviewed. The status of *L. crockeri,* a form endemic to a brackish water lake on Rennell Island (Solomon Islands), is considered and its relationships with *L. laticaudata,* to which it is sometimes regarded as being only subspecifically related, are discussed. Next, the relationships between *Laticauda* species are analysed using both phenetic and phylogenetic methods of analysis. In terms of overall (phenetic) resemblance, *L. colubrina* is closer to the *L. laticaudata/crockeri* lineage than to the divergent *L. semifasciata/schistorhynchus* lineage. Under phylogenetic analysis however, *L. colubrina* emerges as being somewhat transitional between the two lineages. Finally, the wider relationships of *Laticauda* are investigated, again using both phenetic and phylogenetic methods. *Laticauda* clearly shares more overall similarity with terrestrial elapines than with the hydrophiine sea snakes examined. However, when the same data are subjected to phylogenetic analyses (parsimony and compatibility methods) a rather conflicting picture emerges, but, in spite of the incompatibilities, the balance of evidence seems to support the hypothesis of comparatively close association between laticaudines and hydrophiines (a scheme that is also congruent with recent immunological studies).

Malcolm Smith (1926: xi), in his classic work on sea snakes (Hydrophiidae), regarded *Laticauda* as the most primitive sea snake genus and suggested a dual origin of the Hydrophiidae; the Laticaudinae (in which he placed *Laticauda, Aipysurus* and *Emydocephalus*) from Australia and the Hydrophiinae (containing the remaining sea snakes) from Indo-Malaya. Later he appeared to slightly modify his opinion by stating (Smith 1943: 439) that the Laticaudinae and Hydrophiinae 'are united through *Ephalophis'*. Underwood (1967: 110) however mentioned that à case still had to be made that *Laticauda* is related to the other sea snakes and McDowell (1967, 1969, 1972, 1974) has argued that *Laticauda* is not closely related to the true sea snakes (Hydrophiinae including *Aipysurus* and *Emydocephalus)* but represents an independent marine adaptation of a group of elapids comprising the Asiatic coral snakes (*Calliophis, Maticora*), the American coral snakes (*Micrurus* and *Micruroides*) and an elapid from Bougainville, Solomon Islands *(Parapistocalamus)*.

Some workers have accepted McDowell's theory, for example Smith *et al.*(1977) even proposed a radical change in classification with *Laticauda* being placed in the subfamily Elapinae of the family Elapidae and remaining sea snakes being assigned to the subfamily Hydrophiinae of the family Hydrophiidae. Others have, however, regarded the position of *Laticauda* as equivocal e.g. Voris (1977) grouped *Laticauda* and true sea snakes together in the same family (Hydrophiidae) but stated that *Laticauda* is 'a group of very closely related species distinct from all other sea snakes and either represent an independent evolutionary line or a very early separation from all other sea snakes'.

Bull. Br. Mus. Nat. Hist. (Zool.) **50**(2): 127–161 Issued 26 June 1986

Recent immunological evidence (e.g.Cadle & Gorman, 1981; Mao *et al.*, 1983) suggests that *Laticauda* and true sea snakes are relatively closely related although Mao *et al.* (1983: 870) state that 'the Hydrophiinae are much closer immunologically to the Australian elapids than is the genus *Laticauda*'.

In the belief that this somewhat confused picture could possibly be clarified by phylogenetic methods of analysis, the author undertook a study of the morphological characters which bear upon the relationships of *Laticauda* (McCarthy, 1982). While no very clear answer to the central problem was obtained the resulting data set has a number of interesting aspects which are presented here.

Intraspecific variation in *Laticauda*

The genus *Laticauda* has an extensive distribution from the Bay of Bengal through the Indo-Australian area, north to Japan and west to some South Pacific islands (Niue, Tonga and Samoa); there are even unconfirmed reports of the occurrence of one species on the west coast of Central America (Fig. 1).

Five species are currently assigned to the genus although two of these (*L. crockeri* and *L. schistorhynchus*) are regarded by some authorities as being only subspecifically distinct. Two of the species (*L. laticaudata* and *L. colubrina*) together occupy almost the entire known range of the genus. *L. semifasciata* and *L. schistorhynchus* appear very closely related to each other but have peculiarly disjunct distributions (see below). *L. crockeri*, a close relative of *L. laticaudata*, is confined to a land-locked lagoon on Rennell Island, Solomons.

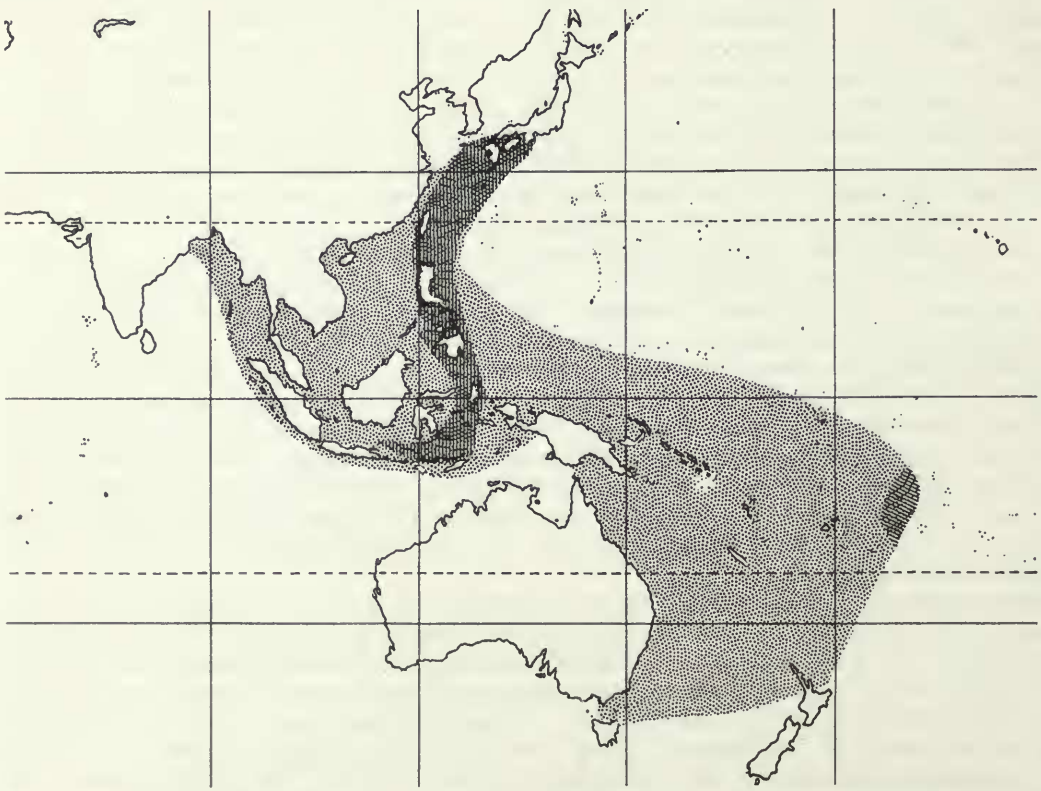
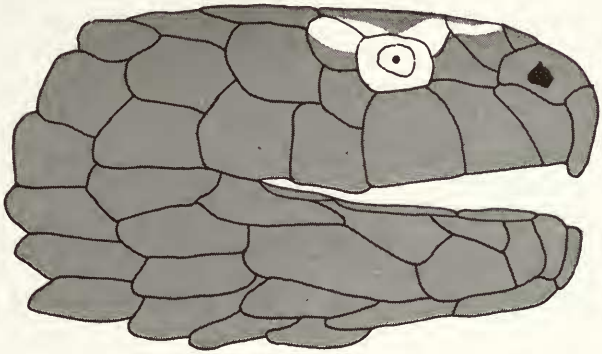


Fig. 1 Distribution of laticaudine sea snakes. Stippled shading = Joint distributions of *Laticauda colubrina* and *L. laticaudata* (there are also some reports of *L. colubrina* from Central America, p. 134). Vertical line shading = Distribution of *L. semifasciata*. Oblique line shading = Distribution of *L. schistorhynchus*. Asterisk = Distribution of *L. crockeri*.

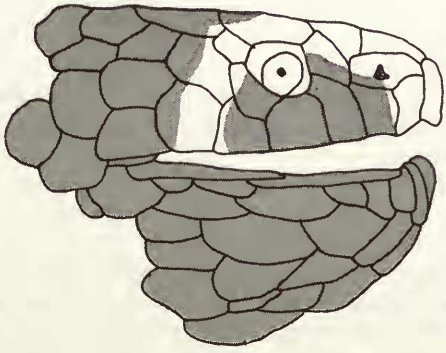
Laticauda laticaudata (Linnaeus, 1758)

A wide-ranging species regarded (e.g. Klemmer, 1963) as comprising two subspecies:- *L. l. laticaudata* (Linnaeus, 1758) from Philippines, Indo-Australian Archipelago, New Guinea, Australia, Oceania and *L. l. affinis* (Anderson, 1871) from India, Malay Peninsula, South China, Taiwan and Ryukyu Retto (Japan).

According to Stejneger (1907: 404) the two forms may be distinguished on colour pattern. *L. laticaudata laticaudata* has a light horse-shoe shaped mark, on top of the head, which bends down behind the eye to reach the lip. In contrast, the light horse-shoe shaped mark in *L. laticaudata affinis* does not curve down behind the eye (Fig. 2). Additional differences between the two forms, cited by Stejneger, include: light coloured rings on belly 4–5 ventrals wide in *L. l. laticaudata* which also has no or one incomplete light ring on the neck; in *L. l. affinis* the light belly rings are 1–3 ventrals wide and there are usually two incomplete light neck rings. Stejneger also commented that the extent to which these characters held good in a large series required investigation.



a



b

Fig. 2 Head coloration in *Laticauda laticaudata*. (a) Typical 'eastern' form (Loo Choo); note that the light mark does not turn down posterior to the eye. (b) Typical 'western' form (Tasmania); note the down-turned light mark.

Table 1. *Laticauda laticaudata*, geographical variation.

Registration number[1]	Locality	Down-turned head-mark[2]	Incomplete neck rings	Number of ventrals in light ring
BM 56·9·4·53	Fiji	+	0	2·3–2·9
BM 77·2·24·18	Duke of York Id.	+	0	3·4–4
BM 1926·11·1·6	Java	+	0	5–5·6
BM 42·11·22·34	New Guinea	+	0	3–3·2
BM 55·11·7·31	San Cristobal	+	0	3·4–3·7
BM 55·10·16·439	Tasmania	+	1	2·7–2·9
BM 59·9·20·70	'Chartaboum' (locality suspect)	+	1	3·2–3·8
BM 1966·309	Aneitum, New Hebrides	+	0	2·7–2·8
BM 1936·2·1·17	Florida, Solomons	+	0	3·6–4·1
BM 42·11·22·32	New Guinea	+	0	2·9–3·5
ZMC 66265	Sydney	+	0	3·5
RML 6272	Ternate	+/−	2	1·95–2·75
RML unreg.	Deli	+/−	1	1·8–2
ZMC 66262	Nicobar	−	2	3–3·5
ZMC 66263	Nicobar	−	2	2·7–3·2
BM 1925·12·8·2	Bengal	−	1	4–4·7
BM 1901·10·23·9	Ishigahi, Loo Choo	−	1	1·4–1·7
BM 87·1·31·36	Loo Choo	−	2	0·3–1·8
RML unreg.	Sika	−	2	2–3
RML 6274a	Menado	−	2	2–2·3
RML 6274b	Menado	−	2	2·5
RML 5898a	Sulawatti	−	2	2·5–2·8
RML 5898b	Sulawatti	−	2	2·0–2·6
RML 10668	Pasir	−	2	1·7–2·2
RML 5503a	Nias	−	2	2·3
RML 5503b	Nias	−	2	1·95–2·2
RML 12628	Ambon	−	1	3·5–4
RML 10669	Soek	−	2	1·7–1·9
RML 7590	Atjeh	−	1	2·2–2·8
RML 12663	Laboean Lembeh	−	2	?
RML 6271	Ambon	−	2	2·2–2·6
RML 12649	Obi	−	2	2–2·5
RML 5218a	Sumatra	−	2	2–2·6
RML 5218b	Sumatra	−	2	2–2·5

[1]BM = British Museum (Natural History), London; RML = Rijksmuseum van Natuurlijke Historie, Leiden; ZMC = Zoologisk Museum, Copenhagen.
[2]+ indicates presence; − indicates absence.

Table 1 shows the distribution of the above characters in the 34 specimens of *L. laticaudata* examined in the present study. It appears that the head pattern can indeed be used to partition *L. laticaudata* broadly into eastern and western populations however some specimens in the intermediate area (Ternate and Deli) show asymmetry, the head mark being down-turned on one side of the head but not on the other. Additional features do not correlate *absolutely* with the condition of the head mark but there is a degree of correspondence; 8 of the 13 specimens that show some down-turning of the head mark also have light body rings that are in excess of three ventrals wide whereas only 3 of the 21 specimens that lack the down-turning have light bands as broad as this. Additionally the number of incomplete neck bands is generally greater in eastern than in western specimens (17 of the 21 eastern forms have two incomplete neck rings whereas

none of the 11 western forms have this condition; the intermediate specimens from Ternate and Deli have two and one incomplete neck rings respectively). If subspecies of *L. laticaudata* are deemed worthy of recognition, which seems unwarranted owing to the apparently clinal nature of the variation between eastern and western forms, Enderman (1970 unpublished ms.) observes that Linnaeus's type of *laticaudata* was probably based on an Asiatic specimen; he would therefore relegate *affinis* (Anderson, 1871) to the synonymy of *L. l. laticaudata*. In this event the name available for the Pacific population appears to be *L. l. muelleri* (Boulenger, 1896).

Laticauda crockeri Slevin, 1934

Endemic to Lake Tegano (= Te-Nggano), Rennell Island, this species resembles *L. laticaudata* in several respects. The main points of difference between the two forms are outlined below:

L. crockeri
1. Midbody scale rows 19; occasionally 21
2. Ventral scales 192–207
3. Strong but variable tendency to melanism; some individuals almost uniformly dark.

L. laticaudata
1. Midbody scale rows invariably 19
2. Ventral scales 219–252
3. Not melanistic, head pattern and body banding always clearly visible.

Slevin's (1934) description of *L. crockeri* was based on one uniformly dark brown specimen, with 21 midbody scale rows, collected in Lake Tegano in 1933. In 1956, Volsøe described a new subspecies from the lake, *L. laticaudata wolffi* based on three individuals all with 19 midbody scale rows and with a degree of melanism i.e. 'head entirely black above and dark brown below' ground colour of body 'dark slate grey dorsally (almost merging with the black bands)'. He further noted that *L. laticaudata wolffi* appeared to differ from Slevin's description of *L. crockeri* in only two respects:- in the number of scale rows (19 vs. 21) and in coloration. In addition, Volsøe reported that *L. colubrina* also occurred in the lake. He therefore described the following situation:

> This freshwater lake is inhabited by no less than three different species of sea snakes all belonging to the same genus *Laticauda* namely:
> 1. *L. colubrina*. The lake population is undifferentiated from the typical form which occurs also along the shores of the island.
> 2. *L. laticaudata wolffi*. Subspecifically distinct from the nominate form which has not been taken from the shores of Rennell Island ...
> 3. *L. crockeri*. An endemic species with unknown relationships to other species of *Laticauda*.

Later, Volsøe (1958) described nine further specimens of *L. 'laticaudata'* from the lake. He recorded that eight had 19 midbody scale rows (like *L. l. wolffi*) whereas one had 21 midbody scale rows reducing to 19 a little distance posteriorly. The aberrant specimen was very dark (and therefore in agreement with the description of *L. crockeri*) but three of the other specimens matched it in colour. He concluded that 'there can be no doubt, therefore, that they all belong to the same form'. The correct name to be applied to the Lake Tegano endemic, following Volsøe (1958) is *L. laticaudata crockeri* with *L. l. wolffi* being reduced to a synonym of that form.

Recently, Cogger (1975: 124) implied that the status of *L. laticaudata wolffi* and *L. crockeri* was uncertain, citing a suggestion by Voris (1969 unpublished thesis) to the effect that '*wolffi* may represent the product of recent hybridization between *crockeri* and immigrant *laticaudata*'. Kharin (1984) treats *L. laticaudata wolffi* and *L. crockeri* as separate entities. However, McCoy (1980: 70) is of the opinion that '*crockeri* and *laticaudata wolffi* are almost certainly synonymous'.

Wolff (1969, 1970) agreed with Volsøe and recognized only two forms from the lake; *L. laticaudata crockeri* and *L. colubrina*. He commented that whilst the lake population of *L. colubrina* appears indistinguishable from individuals occurring outside the lake, '*L. crockeri* has become clearly differentiated from the ancestral form' (Wolff, 1970: 20), suggesting that either *L.*

colubrina is a recent invader or 'for some unknown reason is the only one of the two species which migrates to and from the lake through the subterranean channel'.

Among a large series of *crockeri* collected by him in 1977, McCoy (1980: 70) found that 'most specimens had 19 scale rows at midbody, several had 21 and one individual had 19, 20 and 21 rows in an area around midbody', moreover 'there was no relation between the number of scale rows and the degree of distinction of the dark banding'. In the present study of relatively large series of *Laticauda crockeri* has been examined in the collection in the Zoologisk Museum, Copenhagen (including the holotype and paratypes of *L. l. wolffi*.). The holotype of *L. crockeri* (from the California Academy of Sciences) and a paratype of *L. l. wolffi* in the British Museum (Natural History) have also been available. Table 2 displays the distribution of the supposed diagnostic features of *L. crockeri* and *L. l. wolffi* in this sample. It can be seen that a midbody count of 21 is uncommon (occurring in 2 out of 19 specimens) in the sample of *crockeri* examined. That it is also aberrant is indicated by the complex scale row reduction formulae (given below) of the two specimens recorded as having this count:

Scale row reduction formula of *L. crockeri* (HOLOTYPE) CAS 72001

$$20 \frac{}{5 + 6 \text{ (before first ventral)}} \quad 19 \frac{6 = 6 + 7(82)}{5 = 5 + 6(82)} \quad 21 \frac{6 + 7(83/84)}{6 + 7(84)} \quad 19$$

$$19 \frac{5 = 5 + 6(92), 6 + 7(94), 5 = 5 + 6(97)}{5 = 5 + 6(88), 6 + 7(90), 5 = 5 + 6(96)} \quad 21 \frac{}{6 + 7(100)} \quad 20 \frac{}{5 = 5 + 6(103)} \quad 21$$

$$21 \frac{6 + 7(104)}{} \quad 20 \frac{5 = 5 + 6(108)}{} \quad 21 \frac{6 + 7(112)}{} \quad 20$$

$$20 \frac{5 = 5 + 6(115)}{} \quad 21 \frac{5 + 6(118)}{} \quad 20 \frac{5 = 5 + 6(120)}{} \quad 21$$

$$21 \frac{6 + 7(127)}{6 + 7(126)} \quad 19 \frac{5 + 6(189)}{4 + 5(188)} \quad 17 \frac{v = 2(196)\ 4 + 5(200)}{2 = 2 + 3(202)} \quad 18$$

Scale row reduction formula of specimen ZMC 66134

$$21 \frac{6 + 7(108)}{} \quad 20 \frac{5 = 5 + 6(110)}{} \quad 21 \frac{6 + 7(119), 5 = 5 + 6(120), 6 + 7(124)}{6 + 7(124)} \quad 19$$

$$19 \frac{}{4 = 4 + 5(129)} \quad 20 \frac{}{6 + 7(131)} \quad 19 \frac{}{5 = 5 + 6(134)} \quad 20 \frac{}{6 + 7(139)} \quad 19$$

$$19 \frac{4 + 5(187)}{4 + 5(191)} \quad 17 \frac{}{3 + 4(202)} \quad 16$$

The marked irregularity of the above formulae together with the rare occurrence of 21 midbody scale rows is strong evidence for the atypical nature of the condition.

Complete melanism is also rather rare and not necessarily correlated with the number of midbody scale rows (McCoy, 1980). It seems certain that Volsøe (1958) was correct in regarding *L. crockeri* and *L. l. wolffi* as synonyms.

Whether to treat the endemic form as being only subspecifically distinct from *L. laticaudata* is problematical. *L. laticaudata* and *L. crockeri* certainly resemble each other rather closely in many features that are not shared with other *Laticauda* species e.g. azygous prefrontal scale is absent; first rank of marginal lower lip scales is elongate; usually 19 midbody scale rows; heart tip in a more anterior position than *L. colubrina*; tracheal lung absent; vestigial left lung present (like all *L. laticaudata* and only some *L. colubrina*).

Table 2. *Laticauda crockeri*, scale row reduction and extent of melanism.

Registration number[1]	Abbreviated scale row reduction neck: midbody: vent	Degree of melanism head melanistic/ body melanistic[2]
CAS 72001 (Holotype of *L. crockeri*)	20(19) : 21 : 18	+/+
ZMC 668 (Holotype of *L. l. wolffi*)	19 : 19 : 17	+/−
ZMC 666 (Paratype of *L. l. wolffi*)	? damaged	+/−
ZMC 667 (Paratype of *L. l. wolffi*)	19 : 19 : 16	+/−
BM 1955·1·13·10 (Paratype of *L. l. wolffi*)	21 : 19 : 18	+/−
ZMC 66134	21 : 21 : 16	+/−
ZMC 66135	? damaged	+/+
ZMC 66136	21 : 19 : 16	+/−
ZMC 66137	21 : 19 : 16	−/−
ZMC 66138	19 : 19 : 15	+/+
ZMC 66139	19 : 19 : 17	−/−
ZMC 66140	19 : 19 : 17	−/−
ZMC 66141	19 : 19 : 15	−/−
ZMC 66142	21 : 19 : 16	−/−
ZMC 66293	19 : 19 : 15	−/−
ZMC 66294	21 : 19 : 16	−/−
ZMC 66244	21 : 19 : 17	−/−
ZMC 66245	21 : 19 : 15	−/−
ZMC 66239	19 : 19 : 16	−/−
ZMC 66240	19 : 19 : 17	−/−
ZMC 66237	19 : 19 : 15	−/−

[1]BM = British Museum (Natural History), London; CAS = California Academy of Sciences, San Francisco; ZMC = Zoologisk Museum, Copenhagen.
[2]+ = complete melanism; − = head pattern or body bands visible.

Most of the above characters appear to be relatively primitive and therefore unlikely to be strong indicators of close relationship. However it is also true that very few characters have yet been discovered that can effectively discriminate between *laticaudata* and *crockeri*; only the ventral count seems entirely to do so (192–210 in *crockeri*, 219–252 in *laticaudata*). Additionally, Tamiya, *et al.* (1983), in their analysis of neurotoxins, found that '*L. laticaudata* and *L. crockeri* are very closely related, although there are some genetic differences'. It seems therefore reasonable to suggest that *L. laticaudata* and *L. crockeri* are more closely related to each other than either is to any other extant species. *L. crockeri* may only be a subspecies of *L. laticaudata* but as the forms are allopatric this hypothesis is difficult to confirm.

Voris's (1969: 368–369) hypothesis that an invasion of *L. laticaudata* resulted in hybridization between it and *L. crockeri* to produce *L. laticaudata wolffi* is hardly supported by the evidence. Perhaps the most likely explanation for the situation in Lake Tegano is that a population (possibly of *L. laticaudata*) became isolated when the lake was formed. According to Wolff (1970: 20) the age of the lake as a brackish water body is unknown, 'although it seems probable that the lagoon was cut off from the sea not long after the elevation of the land started in the late Pliocene'. *L. crockeri* may have evolved its pecularities as a result of: selection processes in the lake environment, inheritance from a somewhat aberrant founder population, or genetic drift due to isolation in a small population.

An enigma still remaining to be considered is: why has the *crockeri* population in the lake become distinct whereas *L. colubrina* appears not to have formed a discrete lake form? As mentioned earlier, Wolff (1970) suggests that *crockeri* is unable to navigate through an inferred subterranean passage to the sea whereas *colubrina* is able to do so. However, a simpler explanation is

afforded by knowledge of *L. colubrina*, a species that appears to be more terrestrial in its habits than other species of *Laticauda*. This suggests that *L. colubrina* may be able to cross the high ground surrounding the lake and thus maintain genetic flow with the marine population. Wolff (1970:13) observes that the lake is 'surrounded on all sides by a rim with a width of 0·9–2 km and a continuous height of about 100 m'; the only exception is at the extreme eastern end of the lake where the height of the rim is only 45 m.

The climbing ability of *L. colubrina* is demonstrated by a record of some specimens from Taiwan that were found on top of a solitary coral reef about 50 m high (Mao & Chen, 1980). Although *L. crockeri* 'has been found moving amongst short grass surrounding the lake' (McCoy, 1980: 70) it may be less terrestrial in its habits than *L. colubrina* and a barrier of the dimensions described by Wolff might well prevent it commuting between the lake and the sea.

Laticauda colubrina (Schneider, 1799)

This species has a very widespread distribution which is largely shared with *L. laticaudata*. Additionally there are some reports of *L. colubrina* from Nicaragua (Villa, 1962), Mexico (Alvarez del Toro, 1982) and El Salvador (Villa, pers. comm.). Unfortunately these records are based on material that is no longer available for examination; the presence of *L. colubrina* in tropical America therefore requires substantiation (Villa, pers comm.).*

Through its range, *L. colubrina* shows considerable variation in neck and body coloration and in some aspects in its scalation. Enderman (1970) considers that six populations of *L. colubrina* are worthy of subspecific recognition: (i) New Caledonia; (ii) Fiji, Tonga, Society Islands; (iii) New Hebrides (=Vanuatu), Solomons, Bismarck Archipelago; (iv) Geelvink Baai (northern Irian, New Guinea); (v) Lesser Sunda Islands and S.W. New Guinea to Ryukyus, Japan; (vi) Sumatra, Malaya, Bay of Bengal. The features which Enderman cites to support the recognition of these subspecies comprise mainly relatively minor differences in neck and body banding; he also observes that populations (i)–(iv) usually lack a postmental scale whereas populations (v) and (vi) normally have one (Fig. 3).

Amino acid sequencing of neurotoxins reveals at least three genetically different populations of *L. colubrina*: the difference in the structure of long-chain neurotoxins, between populations from Japan and the Philippines in contrast with those from the Solomons, Fiji and New Caledonia, is

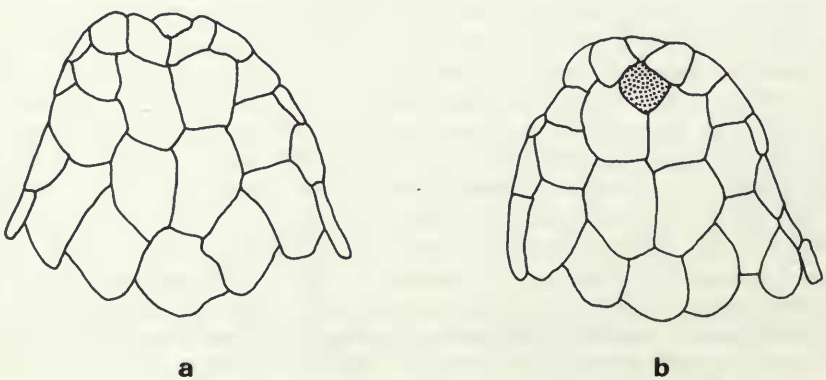


Fig. 3 Chin shields of *Laticauda colubrina*. (a) Typical 'western' form (Solomon Is); postmental scale absent. (b) Typical 'eastern' form (Singapore); postmental scale present (stippled).

*A female specimen in Stuttgart Museum (SMNS-4203) is alleged to have been collected in Guatemala in 1877 (donor unknown); the collecting locality is thought doubtful (Wermuth & Schluter, pers. comm.). In most respects the specimen appears to be a fairly typical western form having a fairly low ventral count (226) and lacking a postmental scale. It has one incomplete light band on its neck and 28 dark bands on its body.

especially well-marked (Tamiya *et al.*, 1983). Very recently a population in Vanuatu, with low ventral scale count and unusual neck coloration, has been studied, which appears to be a distinct species, occurring sympatrically with more typical *L. colubrina*. A related population occurs in the northern part of the Tonga island group (Cogger, pers. comm.).

A full analysis of population variation in *L. colubrina* is beyond the scope of the present study. However, examination of some morphological characters of 72 specimens (Table 3) indicates that, like *L. laticaudata,* the main division appears to be into eastern and western forms. The trend in ventral counts of *L. colubrina* is for them to be generally higher in eastern specimens than western specimens. This tendency in ventral counts is also reflected in some *L. colubrina* literature records. Guinea (1981), for instance, give mean ventral counts of 223 (n = 6) and 228·7 (n = 10), for males and females respectively, from Fiji, whereas Mao & Chen (1980) give mean counts of 231 (n = 9) and 236 (n = 16), for males and females respectively, from Taiwan.

Some other characters are only variably present in *L. colubrina* i.e. azygous prefrontal scale and vestigal left lung, but these features appear to show no obvious correlation with geographic distribution.

Table 3. *Laticauda colubrina*; geographical variation in the ventral counts and in postmental presence.

Locality	Sex	n	Ventrals range (mean)	Postmental percentage presence
Japan	♀	1	249·5	100%
Taiwan	♂	1	239	100%
Philippines	♂	1	236	100%
	♀	1	249	100%
Malaya & Thailand	♂♂	6	224–240·5 (233·75)	66·7%
	♀♀	5	234–248 (243·4)	60%
Andamans	♀	1	235	100%
Sumatra	♂♂	3	223–224 (223·33)	66·7%
	♀	1	240	100%
Borneo	♂	1	230	0
Java Sea	♀	1	227	100%
Sulawesi	♂	1	228	100%
	♀	1	232	100%
Moluccas	♂	1	226	100%
	♀	1	238	100%
Lesser Sunda Is.	♂♂	2	226–228 (227)	50%
	♀	1	234	100%
New Guinea	♂♂	3	232–240·5 (235·17)	66·7%
	♀♀	3	229–240 (235)	100%
Solomon Is.	♂♂	9	218–229 (222)	0
	♀♀	12	220–233 (226·79)	0
New Caledonia	♂	1	221	0
	♀	1	224	0
New Hebrides[1]	♂♂	3	216–225·5 (219)	0
	♀	1	213	0
Fiji & Tonga	♂♂	4	224–226 (225)	0
	♀♀	3	229–236 (232·67)	0
Australia & New Zealand	♂♂	2	214·5–219 (216·75)	0
	♀	1	231	0

[1]Two distinct forms are recorded from New Hebrides (= Vanuatu), one ('new form') with low ventral count and unusual neck coloration, the other with higher ventral counts and more typical *colubrina* coloration (Cogger, pers. comm.). The ♂ with 216 ventrals and the ♀ with 213 ventrals, in the above series, appear assignable to this 'new form'.

Laticauda semifasciata (Reinwardt in Schlegel, 1837) and *Laticauda schistorhynchus* (Günther, 1874)

L. semifasciata and *L. schistorhychus* closely resemble each other, indeed they mainly appear to have only *average* differences, i.e. number of ventrals and bands on the body and in maximum adult size (Smith, 1926).

Tamiya *et al.* (1983: 447) analysed neurotoxins and found that *L. semifasciata* and *L. schistorhynchus* are genetically homogeneous as far as these components are concerned. Guinea, Tamiya & Cogger (1983) concluded that there is no justification for treating *L. semifasciata* and *L. schistorhynchus* as separate species.

There do indeed seem reasonable grounds for considering the two forms conspecific. However, there is no proof that they interbreed; *L. semifasciata* and *L. schistorhynchus* are completely allopatric being separated by an enormous gap. *L. semifasciata* has been recorded from South Japan, Riu Kius, Philippines, Moluccas and Lesser Sunda Islands, whereas *L. schistorhynchus* is found in the Pacific at Niue, Tonga and Samoa. There is however a single dubious record of *L. schistorhynchus* from 'Bertrand' Island (=Tendanye Island), New Guinea (a specimen in the Hamburg Museum cited by Smith 1926).

The circumstances that led to splitting of *L. semifasciata/schistorhynchus* populations are unknown but it is possible that competition from similar forms might, at least in part, be responsible. In the area where members of the *semifasciata* group are absent, for instance, there occur members of the genus *Aipysurus*. *Aipysurus* comprises several species of hydrophiines that are confined (with the exception of *A. eydouxi*) to the continental shelf waters of Australia and New Guinea, they also occur in parts of the extreme south west Pacific Ocean (Cogger, 1975: 72). This diversity of shallow-water sea snakes might well fill niches that are thus unavailable for the *semifasciata* group; this theory might also account for the relative rarity of other *Laticauda* species in Australian waters.

Characters examined—Data matrix

The Elapidae are a relatively large family (comprising 244 species according to Dowling & Duellman, 1978; McCarthy, 1985), therefore there are practical difficulties in examining all elapid species for many characters that might have relevance to the question of laticaudine relationship.

Table 4. Survey of *Laticauda* 'special features'.

	Character state numbers (derived conditions)[2]						
Group[1]	7·1 or 7·2	9	25·2	26·2 or 26·3	46·2	48	65
Laticauda	+	+	+	+	+	+	+
Hydrophiines	+	−	−	+	+	+	−
African & Middle Eastern elapines	+	−	+	−	−	−	−
Asiatic elapines	−	−	+	−	+	+	−
American elapines	−	−	+	+	+	−	−
New Guinea & Solomons elapines	−	−	+	+	−	−	−
Australian elapines	−	−	−	+	−	−	−

[1] + indicates the presence of a state in at least some members of the group concerned.
[2] Character states are described in Table 5.

In order to cope with this problem it was decided to carry-out methods of analysis on a sample comprising all species of *Laticauda* together with a selection of ten other elapids.

The non-laticaudines in the sample were selected on the basis of a survey of the Elapidae for seven characters of *Laticauda* that were hitherto believed to have a restricted distribution outside the genus. The results of the survey are summarised in Table 4. The resulting sample of elapids was then examined for 45 binary and 20 multistate characters (Table 5) and a data matrix was compiled (Table 7).

Polarity of the characters (Table 6) was mainly determined on the criterion of out-group comparison i.e. if a character state is common (widespread) among Caenophidia (higher snakes), it is regarded as primitive within the Elapidae. A more detailed account of the characters analysed, and polarity criteria used, is given by McCarthy (1982).

The problem of relationship is considered from a number of perspectives i.e. from the viewpoint of overall ('phenetic') resemblance (see Sneath & Sokal, 1973) and from the viewpoint of various phylogenetic ('cladistic' or 'evolutionary') approaches (see review by Felsenstein, 1982).

Two basic levels of affinity will be considered here: (*a*) The relationships of *Laticauda* species to each other. (*b*) The relationships of the genus *Laticauda* to other elapids.

Interspecific relationships within genus *Laticauda*

Phenetic analysis

Overall (phenetic) similarity can be measured in many ways; one of the most commonly used coefficients is the simple-matching coefficient and it is this expression of resemblance that is used here. Simple-matching coefficients are calculated (e.g. Sneath & Sokal, 1973: 132) according to the formula:

$$\text{Ssm} = \frac{m}{n}$$

(where m = the number of matches between pairs of taxa and n = the number of characters)

The overall similarity matrix is shown in Table 8. From this the scheme illustrated in Fig. 4 was constructed using the 'unweighted pair-group' method of clustering (as discussed by Sneath & Sokal, 1973: 230–234).

From Figure 4 it can be seen that *Laticauda semifasciata* and *L. schistorhynchus* are very close to each other phenetically; similarly *L. crockeri* and *L. laticaudata* cluster together. *L. colubrina* resembles *L. laticaudata/crockeri* more than it does *L. semifasciata/L. schistorhynchus*. Overall, the topology is the same as in the phenogram presented by Voris (1977: 91) who also used simple matching coefficients on his data.

Phylogenetic analysis

Phylogenetic (cladistic) analysis involves considering the relationships between taxa in terms of shared derived characters ('synapomorphies'). Reference to the data matrix (Table 7) shows that, when only derived states are considered, there is a conflict between 9 states (7·2; 12·1; 29; 32; 56; 57·2; 58; 60; 64·2) supporting the association of *L. colubrina* with the *L. laticaudata* lineage and 4 states (1·1; 8·2; 14; 15) supporting the clustering of *L. colubrina* with the *semifasciata* lineage. The principle of parsimony ('democratic method' Arnold, 1981: 21) leads one to accept the scheme that is supported by most evidence i.e. the same topology as suggested by phenetic analysis (Fig. 4) with *colubrina* associated with *laticaudata* and *crockeri*. However 6 of the 9 states supporting this association have rather arbitrary polarity determinations (12·1; 29; 32; 58; 60; 64·2) and perhaps should not be used as primary evidence. If arbitrarily scored states are discounted, the balance of evidence shifts marginally in favour of a scheme associating *colubrina* with the *semifasciata* lineage. Two of the 4 states supporting the association of *colubrina* with *semifasciata* are variable the primitive state occurring in some individuals i.e. in *colubrina*, the azygous prefrontal

Table 5.

Summary of character states included in matrix			Additive binary codings (where relevant)	
1.1. Azygous prefrontal shield	0	Absent		
	1	Present		
1.2. Head shield fragmentation	0	Absent		
	1	Present		
2. Horizontal division of rostral	0	Absent		
	1	Present		
3. Nostril position	0	Lateral		
	1	Dorsal		
4. Internasal scales	0	Present		
	1	Absent	5·1	5·2
5. Anterior temporals	0	One or two	0	0
	1	None	1	0
	2	Three	0	1
			6·1	6·2
6. Infralabial formula	0	7(4 + 3)	0	0
	1	6(4 + 2)	1	0
	2	8/9(4 + 4/5)	0	1
			7·1	7·2
7. Marginal lower lip scales	0	None	0	0
	1	Present (one rank)	1	0
	2	Present (two ranks)	1	1
			8·1	8·2
8. Scale rows (midbody)	0	14–21	0	0
	1	10–13	1	0
	2	c.21 or over	0	1
9. Nasal vestibule	0	Smooth lining		
	1	Rugose/papillate lining		
10. Tail shape	0	Rounded		
	1	Laterally compressed		
			11·1	11·2
11. Heart position	0	19–28% ventral count	0	0
	1	29–32% ventral count	1	0
	2	> 33% ventral count	1	1
			12·1	12·2
12. Heart-liver distance	0	> 6% ventral count	0	0
	1	4–5% ventral count	1	0
	2	< 4% ventral count	1	1
13. Heart-systemic arch gap	0	< 2% ventral count		
	1	> 2% ventral count		
14. Vestigial left lung	0	Present		
	1	Absent		
15. Tracheal lung	0	Absent		
	1	Present		
			16·1	16·2
16. Pulmonary air sac	0	Flimsy (not extending to cloaca)	0	0
	1	Muscular (not extending to cloaca)	1	0
	2	Muscular (extending within 5% ventral count from cloaca)	1	1
			17·1	17·2
17. Liver size	0	< 23% ventral count	0	0
	1	23–29% ventral count	1	0
	2	> 40% ventral count	1	1

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)		
18. Liver: vena cava position	0	Central for at least short distance			
	1	Lateral			
19. Kidney: furthest extent	0	More posterior than 90% ventral count			
	1	Less than 90% ventral count			
20. Renal artery pattern	0	1 + 1			
	1	2 + 1 or greater			
			21·1	21·2	
21. Hemipenial calyces	0	Distal calyces	0	0	
	1	Distal & proximal calyces	1	0	
	2	Calyces absent	0	1	
			23·1	23·2	
23. Sulcus bifurcation	0	Significant	0	0	
	1	Only at tip of organ	1	0	
	2	Sulcus simple	1	1	
24. Hemipenis shape	0	Distinctly forked			
	1	Slightly bilobed or simple			
			25·1	25·2	
25. Venom gland shape	0	Rounded; confined to temporal area	0	0	
	1	Extends posteriorly into the body cavity	1	0	
	2	Down-turned posterior corner	0	1	
			26·1	26·2	26·3
26. 'Superficialis' muscle origin	0	Narrow	0	0	0
	1	Broad (not reaching quadrate)	1	0	0
	2	Broad (attaching onto quadrate)	1	1	0
	3	Quadrate head isolated from rest of muscle	1	1	1
27. 'Superficialis' muscle (interruption)	0	Passes uninterrupted around venom gland			
	1	Divided into dorsal and ventral portions			
			28·1	28·2	
28. 'Superficialis' muscle (aponeuroses)	0	No aponeurotic origin	0	0	
	1	Narrow aponeurotic origin	1	0	
	2	Broad aponeurotic origin	1	1	
29. 'Medialis' muscle (quadrate origin)	0	Absent			
	1	Present			
30. 'Medialis' muscle (insertion at mouth corner)	0	Present			
	1	Absent			
31. 'Profundus' muscle	0	Simple			
	1	Divided into anterior & posterior portions			
32. Levator pterygoidei origin	0	Confined to parietal			
	1	Part origin from post-orbital			
33. Protractor pterygoidei, Retractor vomeris and Retractor pterygoidei origins	0	Spread			
	1	Compact-arising from 'pinched' area			
34. Cutaneous muscle in head region	0	Thin			
	1	Thick			
35. Quadrato-maxillary ligament	0	Narrow anteriorly			
	1	Broad anteriorly			
36. Geniohyoideus muscle	0	Extends onto and anterior to lingual process of hyoid			
	1	Not extending onto hyoid lingual process			

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)		
37. Int. mand. post. muscle	0	Not attaching to hyoid lingual process			
	1	Attaching onto hyoid lingual process			
38. Transversus branchialis muscle	0	Not attaching to hyoid lingual process			
	1	Attaching onto hyoid lingual process			
39. Genioglossus muscle	0	With both lateral and medial heads			
	1	With lateral head only			
40. 'Geniomucosalis' muscle	0	Absent			
	1	Present			
			41·1	41·2	
41. Dentary dorsal and ventral extensions	0	Dorsal > Ventral	0	0	
	1	Dorsal = Ventral	1	0	
	2	Dorsal < Ventral	1	1	
42. Parietal and frontal bones	0	Separate beneath optic fenestra			
	1	Meet beneath optic fenestra			
43. Parietal medial crest	0	Absent			
	1	Present			
44. Posterior vidian foramen	0	Exposed			
	1	Roofed-over			
			45·1	45·2	45·3
45. Anterior vidian foramen	0	In parietal or on basisphenoid/ parietal suture	0	0	0
	1	Within basisphenoid	1	0	0
	2	(Two)–one between basisphenoid & parietal; the other just inside the basisphenoid	0	1	0
	3	(Two)–both within the basisphenoid	1	0	1
			46·1	46·2	
46. Optic/opthalmic foramina	0	Single foramen	0	0	
	1	Incompletely separated foramina	1	0	
	2	Double foramina	1	1	
47. Subcaudals	0	Paired			
	1	Single			
48. Caudal haemapophyses	0	Not fusing distally			
	1	Fusing distally			
49. Palatine medial wing	0	Present			
	1	Absent			
50. Palatine lateral process	0	Present			
	1	Absent			
			51·1	51·2	51·3
51. Palatine/Pterygoid articulation	0	Simple	0	0	0
	1	Disjunct	1	0	0
	2	Saddle-joint	0	1	0
	3	Palatine strongly overlapping mesial and lateral faces of pterygoid	0	1	1
52. Pterygoid/Palatine dorsal overlap	0	Pterygoid not overlapping Palatine			
	1	Pterygoid overlapping Palatine			
53. Foramen in palatine bone (lateral process)	0	Present			
	1	Absent			
			54·1	54·2	
54. Maxilla anterior extension	0	Maxilla extends > Palatine	0	0	
	1	Maxilla extends = Palatine	1	0	
	2	Maxilla extends	1	1	

Table 5. *cont.*

Summary of character states included in matrix			Additive binary codings (where relevant)			
55. Postorbital bone	0	Present				
	1	Absent				
56. Parietal ridge and venom gland anchoring ligament	0	Absent				
	1	Present				
			57·1	57·2	57·3	57·4
57. Prefrontal-frontal articulation	0	Oblique	0	0	0	0
	1	Anterior and lateral (square)	1	0	0	0
	2	Anterior	0	1	0	0
	3	Lateral	0	0	1	0
	4	Anterior and lateral (round)	0	0	0	1
58. Palatine teeth number	0	5·5–23·49				
	1	0–5·49				
59. Pterygoid teeth number	0	6·5–27·49				
	1	0–6·49				
60. Anterior portion of skull	0	46·7–58·6%				
	1	38·7–46·6%				
61. Relative length of quadrate	0	21·0–52·9%				
	1	13·0–20·9%				
62. Relative length of compound	0	51·8–67·7%				
	1	67·8–91·7%				
63. Relative length of dentary	0	46·8–67·7%				
	1	25·8–46·7%				
			64·1	64·2		
64. Relative length of supratemporal	0	17·3–45·2%	0	0		
	1	45·3–59·3%	1	0		
	2	3·3–17·2%	0	1		
65. Palatal pocket	0	Absent				
	1	Present				

scale (character 1·1) is absent in some individuals also a vestigial left lung (character 14) is variably present. A possible explanation is that such characters may have been variable in ancestral *Laticauda*, became relatively fixed in *semifasciata* and *laticaudata* lineages but remain variable in *L. colubrina*; a similar scenario is postulated by Arnold (1981: 19).

In conclusion, *L. colubrina* appears to be, in some ways, transitional between the *L. laticaudata* lineage and the divergent *L. semifasciata* lineage and cannot be unequivocally associated with either group on the basis of a phylogenetic analysis of its morphological characters. Biochemical evidence seems consistent with this conclusion. In terms of albumin immunological distance (Cadle & Gorman, 1981; Mao *et al.*, 1983), *L. semifasciata* appears rather divergent although, in tests with antisera to *L. semifasciata, L. colubrina* emerges as slightly closer to *L. semifasciata* than is *L. laticaudata*.

With regard to karyology, Gorman (1981) finds that *L. colubrina* has a diploid count of 34 which he believes corresponds with the primitive elapid condition; *L. laticaudata* and *L. semifasciata* have higher counts (40 and 38 respectively) and these are assumed to have evolved via centric fissions.

Kharin (1984) has recently suggested that *L. semifasciata* and *L. schistorhynchus* are sufficiently different from other *Laticauda* species to warrant being placed in a separate genus *(Pseudolaticauda)*. The above evidence demonstrates that while the *L. semifasciata* lineage is

Table 6.

Polarity patterns

A. 0 ——→ 1
Characters with pattern A:-
1·1,1·2,2,3,4,9,10,13,14,15,18,19,20,24,27,29,30,31,32,33,34,35,36,37,38, 39,40,42,43,44,47,48,49,50,52,53,55,56,58,59,60,61,62,63,65.

B. 0 ——→ 1 ——→ 2
Characters with pattern B:-
7,11,12,16,17,23,28,41,46,54.

C. 0 ——→ 1 ——→ 2 ——→ 3
Character with pattern C:-
26.

D. 1 ←—— 0 ——→ 2
Characters with pattern D:-
5,6,8,21,25,64.

E. 1 ←—— 0 ——→ 2 ——→ 3
Character with pattern E:-
51.

F. 3 ←—— 1 ←—— 0 ——→ 2
Character with pattern F:-
45.

G. 2 ←——
0 ——→ 3
1 ←——
——→ 4
Character with pattern G:-
57.

indeed divergent from the other *Laticauda* lineages it appears possible that *L. colubrina* is phylogenetically closer to *L. semifasciata* than it is to *L. laticaudata*, a relationship that would be obscured if *L. colubrina* and *L. semifasciata* were placed in different genera. It is therefore thought best to here retain the genus *Laticauda* in its former broad sense.

Wider relationships of genus *Laticauda*

Phenetic analysis

Simple matching coefficients and unweighted pair group clustering were used to depict phenetic relationships between all the elapids in the sample (Table 8 and Fig. 4).

Laticauda and other sea snakes appear to share only a relatively low level of phenetic similarity (see also Voris, 1977: 91). Additionally *Laticauda* shares more overall similarity with the terrestrial elapines in the sample than with the hydrophine sea snakes.

Phylogenetic analyses

Wagner Parsimony

The program used in the present study is Farris' 'Advancement sequenced Wagner Program phase AF, version 1/4/69'. The data matrix (Table 7) is modified for Wagner analysis to the extent that variable states are treated as derived (state 1) and unrecordable states are scored as primitive (0). The order of input in Farris' algorithm is governed by advancement-indices; taxa with the smallest number of derived characters being incorporated first, those with the greatest

The numbers in subsequent figures and tables refer to the following taxa:

1 *Laticauda laticaudata*
2 *Laticauda crockeri*
3 *Laticauda colubrina*
4 *Laticauda semifasciata*
5 *Laticauda schistorhynchus*
6 *Parapistocalamus hedigeri*
7 *Calliophis macclellandii*
8 *Calliophis japonicus*
9 *Maticora bivirgata*
10 *Micrurus surinamensis*
11 *Micrurus lemniscatus*
12 *Micrurus psyches*
13 *Ephalophis greyi*
14 *Aipysurus fuscus*
15 *Bungarus flaviceps*

Table 7. Character state matrix
The species are represented by the identification numbers given in caption to Fig. 4. Where a derived state is only variably present, this is indicated by 'V'; where data are missing or otherwise unrecordable '–' is used. Character state numbers preceded by '–' indicates those states for which polarity assessments are rather arbitrary.

	Character nos.																		
	1·1	1·2	2	3	4	5·1	5·2	6·1	6·2	7·1	7·2	8·1	8·2	9	10	11·1	11·2	–12·1	12·2
1	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
2	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1	0
3	V	0	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	1	1
4	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0
5	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0
6	0	0	0	0	0	V	0	1	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	0
8	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
9	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	1	1
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
13	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	1	0
14	V	1	0	1	1	0	V	0	1	1	0	0	0	0	1	1	1	1	1
15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1

Table 7. *cont.*

	−13	14	15	16·1	16·2	−17·1	−17·2	−18	−19	−20	−21·1	−21·2	−23·1	−23·2	−24	25·1	25·2	26·1	26·2
1	0	0	0	1	0	1	0	1	1	0	0	0	1	0	1	0	1	1	1
2	1	0	0	1	0	1	0	1	1	0	0	0	1	V	1	0	1	1	1
3	0	V	1	1	0	1	0	0	1	0	0	0	0	0	1	0	1	1	1
4	1	1	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1
5	1	1	1	1	0	1	0	0	1	0	1	0	1	0	1	0	1	1	1
6	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	1
7	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0
8	0	1	1	0	0	1	0	0	0	1	0	1	1	1	1	0	0	0	0
9	1	1	0	0	0	1	0	0	0	1	0	0	1	0	1	1	0	–	–
10	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	1	1
11	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	1
12	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	0
13	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
14	1	1	1	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
15	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
	26·3	27	28·1	28·2	−29	−30	−31	−32	33	34	35	36	37	38	39	40	41·1	41·2	42
1	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	V
2	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0
3	0	1	0	0	1	0	0	1	0	0	0	1	1	1	0	0	1	1	0
4	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0
5	1	1	0	0	0	1	0	0	1	1	1	1	1	1	0	0	1	1	0
6	0	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
7	0	1	0	0	0	1	1	–	0	0	0	0	0	0	0	0	1	1	0
8	0	1	0	0	1	1	1	–	0	0	0	0	0	0	0	0	0	0	0
9	–	–	–	–	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0
10	0	1	0	0	1	0	0	–	0	0	0	0	0	0	0	0	1	1	0
11	0	1	1	1	1	1	0	–	0	0	0	0	0	0	0	0	1	1	0
12	0	1	1	0	1	0	0	–	0	0	0	0	0	0	0	0	1	1	0
13	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
14	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1
15	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0

	–43	44	45·1	45·2	45·3	46·1	46·2	47	48	49	50	51·1	51·2	51	52	53	54·1	54·2	55
1	1	0	0	0	0	1	1	0	V	1	0	0	1	0	0	V	0	0	0
2	1	V	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
3	1	0	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
4	1	V	0	0	0	1	1	0	V	1	0	0	1	0	0	0	0	0	0
5	1	0	0	0	0	1	0	0	V	1	0	0	1	0	0	0	0	0	0
6	0	0	1	0	1	0	0	0	0	0	1	0	1	1	1	–	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	1	V	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1
9	1	0	0	0	0	1	1	0	0	0	1	0	0	0	0	–	0	0	0
10	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
11	1	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1
12	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1
13	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	–	1	1	0
14	0	V	0	1	0	1	1	1	1	1	1	0	1	0	0	–	0	0	0
15	1	1	1	0	0	1	1	V	0	0	0	0	0	0	1	0	1	1	0

	56	57·1	57·2	57·3	–58	59	–60	–61	–62	–63	–64·1	–64·2	65
1	1	0	1	0	1	0	V	0	1	1	0	V	1
2	1	0	1	0	1	0	0	0	1	1	0	0	1
3	1	0	1	0	V	0	1	0	1	1	0	V	1
4	0	1	0	0	0	0	0	0	1	1	0	0	1
5	0	1	0	0	0	0	0	0	1	1	0	0	1
6	0	0	0	0	0	0	0	1	0	1	1	0	0
7	1	0	1	0	0	1	0	1	0	1	0	0	0
8	1	0	1	0	0	0	1	0	0	1	1	0	0
9	1	0	1	0	0	1	0	1	1	1	0	0	0
10	1	0	1	0	0	0	0	0	1	1	0	0	0
11	1	0	1	0	0	1	0	0	1	1	0	0	0
12	1	0	1	0	0	1	0	1	1	1	0	0	0
13	1	0	0	1	0	0	1	0	0	0	0	0	0
14	1	0	0	1	0	0	0	0	0	1	0	0	0
15	1	1	0	0	0	0	0	0	0	0	0	0	0

Table 8. Overall similarity matrix (simple matching coefficients).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
15	573	584	573	567	551	602	722	693	726	676	688	676	665	534
14	528	540	597	534	523	489	534	523	530	500	466	500	665	
13	511	528	540	511	517	540	563	603	549	575	540	529		
12	642	631	597	511	528	707	841	756	753	932	898			
11	676	665	631	591	585	695	761	722	753	920				
10	688	676	642	580	597	730	795	778	716					
9	598	616	604	561	555	701	827	710						
8	591	597	568	534	545	632	801							
7	585	585	551	511	528	695								
6	563	568	489	574	591									
5	725	747	725	978										
4	730	758	730											
3	865	848												
2	949													

Taxa are represented by the identification numbers given in caption to Fig. 4.

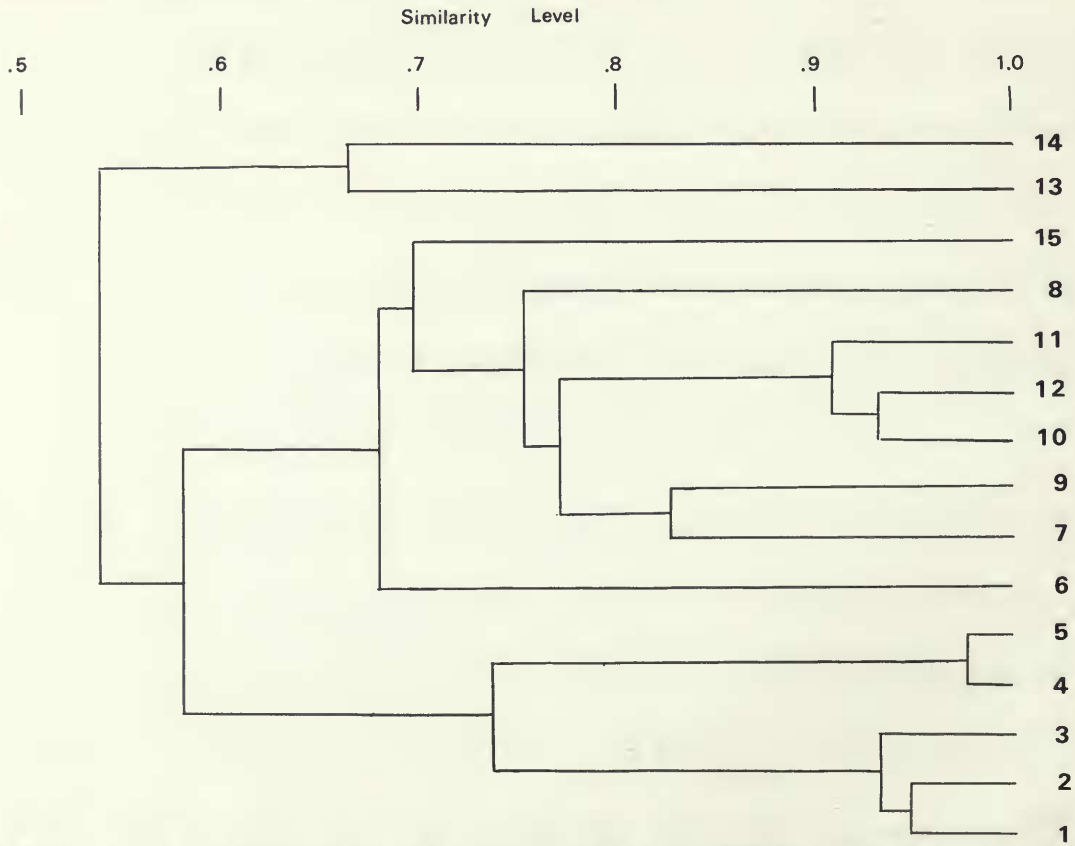


Fig. 4 Dendrogram based on overall similarity (using simple matching coefficients and the unweighted pair group method of clustering). Numbers indicate the following taxa: 1 *Laticauda laticaudata;* 2 *Laticauda crockeri;* 3 *Laticauda colubrina;* 4 *Laticauda semifasciata;* 5 *Laticauda schistorhynchus;* 6 *Parapistocalamus hedigeri;* 7 *Calliophis macclellandii;* 8 *Calliophis japonicus;* 9 *Maticora bivirgata;* 10 *Micrurus surinamensis;* 11 *Micrurus lemniscatus;* 12 *Micrurus psyches;* 13 *Ephalophis greyi;* 14 *Aipysurus fuscus;* 15 *Bungarus flaviceps.*
The cophenetic correlation coefficient of this dendrogram is 0·9425.

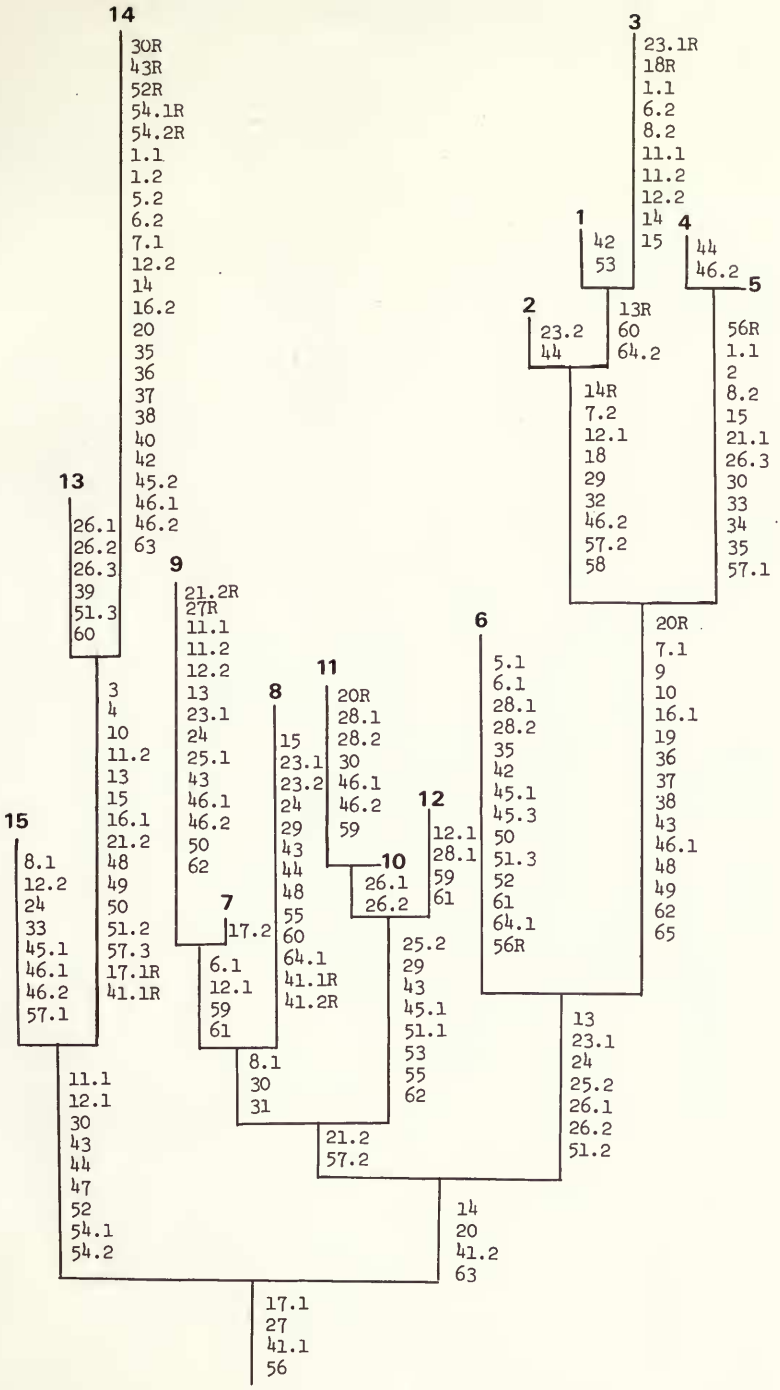


Fig. 5a

Fig. 5 Wagner tree runs. Taxon numbers as in Fig. 4. Character state transformations marked along branches; 'R' following a character number indicates that a reversal has been hypothesized. **(a)** Run 1; entire data set, advancement-index sequenced. **(b)** Run 2; entire data set, taxa in order of Le Quesne test labelling. **(c)** Run 3; 'arbitrary' characters excluded, advancement-index sequenced. **(d)** Run 4; 'arbitrary' characters excluded; taxa in order of Le Quesne test labelling.

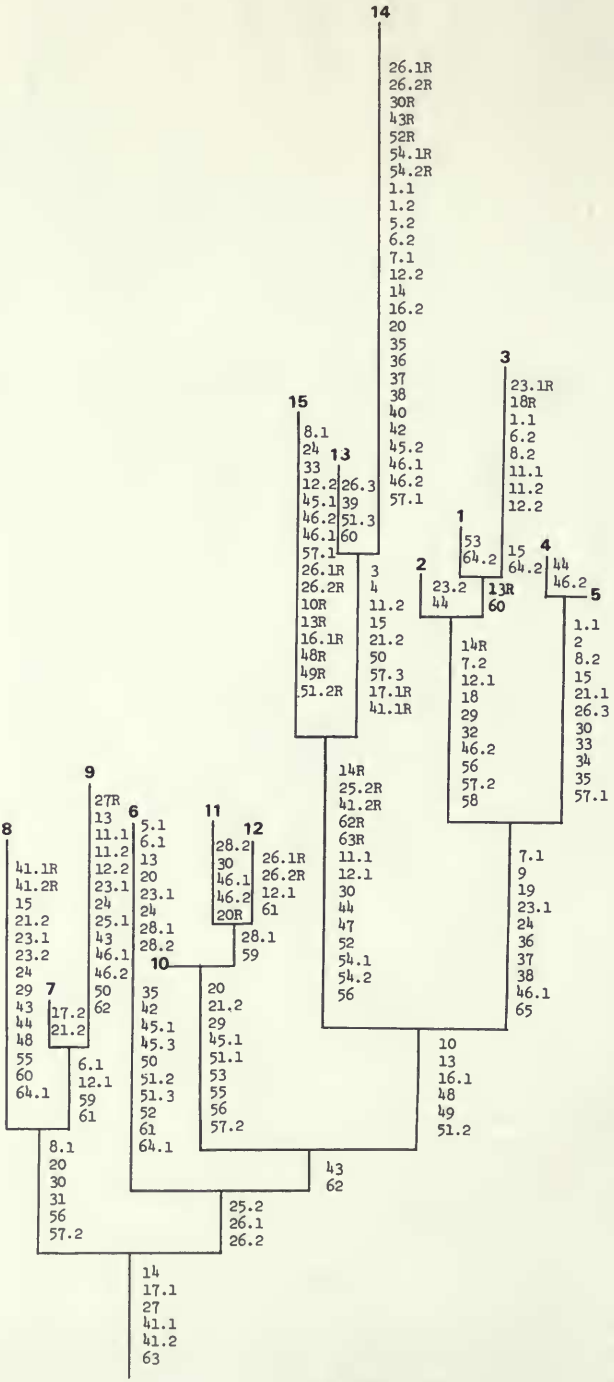

14
26.1R
26.2R
30R
43R
52R
54.1R
54.2R
1.1
1.2
5.2
6.2
7.1
12.2
14
16.2
20
35
36
37
38
40
42
45.2
46.1
46.2
57.1
3
23.1R
18R
1.1
6.2
8.2
11.1
11.2
12.2
15
64.2
1
53
64.2
2
23.2
44
13R
60
4
44
46.2
5
1.1
2
8.2
15
21.1
26.3
30
33
34
35
57.1
14R
7.2
12.1
18
29
32
46.2
56
57.2
58
7.1
9
19
23.1
24
36
37
38
46.1
65
15
8.1
24
33
12.2
45.1
46.2
46.1
57.1
26.1R
26.2R
10R
13R
16.1R
48R
49R
51.2R
13
26.3
39
51.3
60
3
4
11.2
15
21.2
50
57.3
17.1R
41.1R
14R
25.2R
41.2R
62R
63R
11.1
12.1
30
44
47
52
54.1
54.2
56
10
13
16.1
48
49
51.2
9
27R
13
11.1
11.2
12.2
23.1
24
25.1
43
46.1
46.2
50
62
6
5.1
6.1
13
20
23.1
24
28.1
28.2
35
42
45.1
45.3
50
51.2
51.3
52
61
64.1
11
28.2
30
46.1
46.2
20R
12
26.1R
26.2R
12.1
61
28.1
59
10
20
21.2
29
45.1
51.1
53
55
56
57.2
8
41.1R
41.2R
15
21.2
23.1
23.2
24
29
43
44
48
55
60
64.1
7
17.2
21.2
6.1
12.1
59
61
8.1
20
30
31
56
57.2
43
62
25.2
26.1
26.2
14
17.1
27
41.1
41.2
63

Fig. 5b

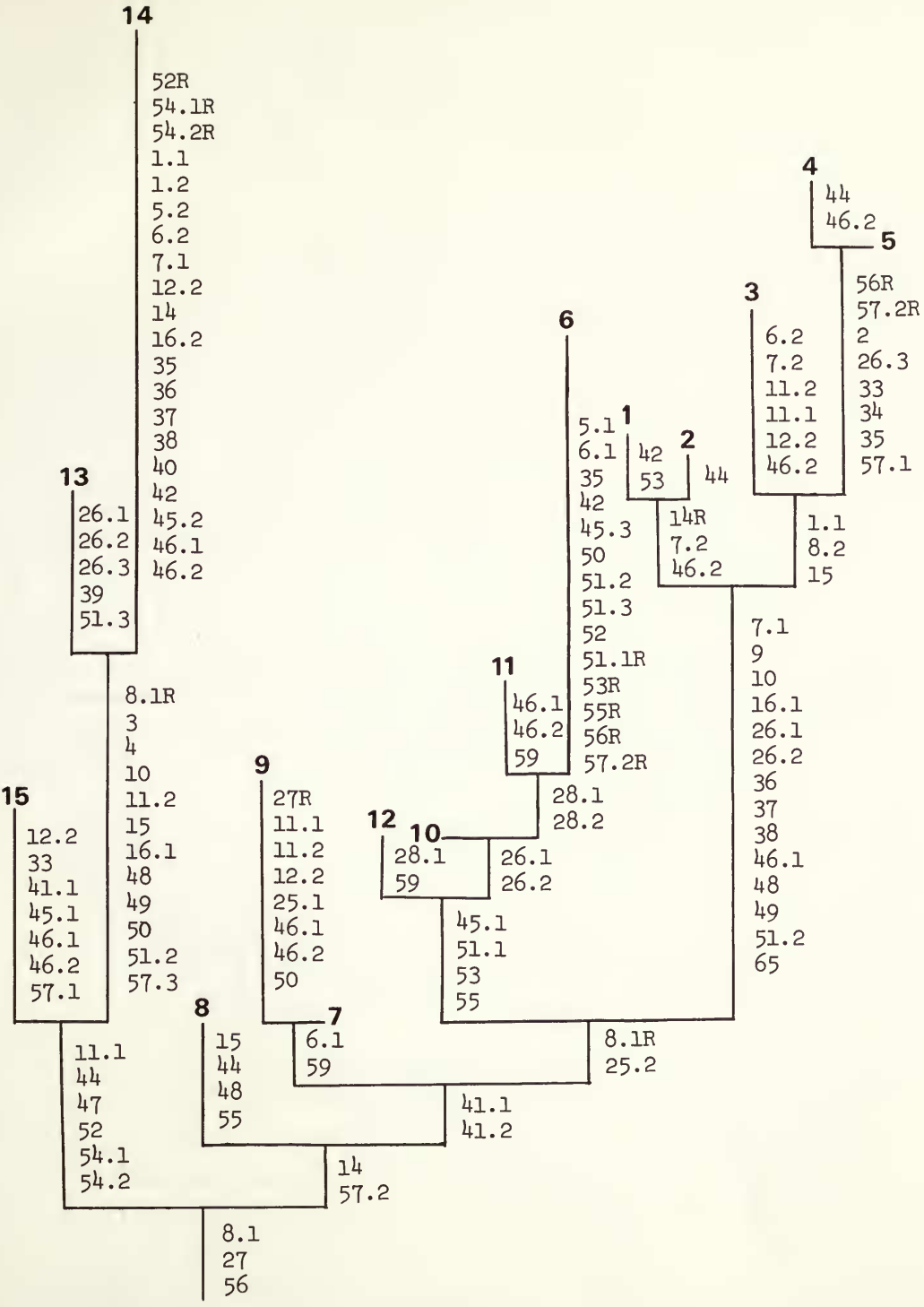

14
52R
54.1R
54.2R
1.1
1.2
5.2
6.2
7.1
12.2
14
16.2
35
36
37
38
40
42
45.2
46.1
46.2
13
26.1
26.2
26.3
39
51.3
8.1R
3
4
10
11.2
15
16.1
48
49
50
51.2
57.3
15
12.2
33
41.1
45.1
46.1
46.2
57.1
11.1
44
47
52
54.1
54.2
8
15
44
48
55
9
27R
11.1
11.2
12.2
25.1
46.1
46.2
50
7
6.1
59
14
57.2
8.1
27
56
41.1
41.2
8.1R
25.2
12
28.1
59
10
26.1
26.2
45.1
51.1
53
55
11
46.1
46.2
59
28.1
28.2
6
5.1
6.1
35
42
45.3
50
51.2
51.3
52
51.1R
53R
55R
56R
57.2R
1
42
53
2
44
14R
7.2
46.2
7.1
9
10
16.1
26.1
26.2
36
37
38
46.1
48
49
51.2
65
3
6.2
7.2
11.2
11.1
12.2
46.2
1.1
8.2
15
4
44
46.2
5
56R
57.2R
2
26.3
33
34
35
57.1

Fig. 5c

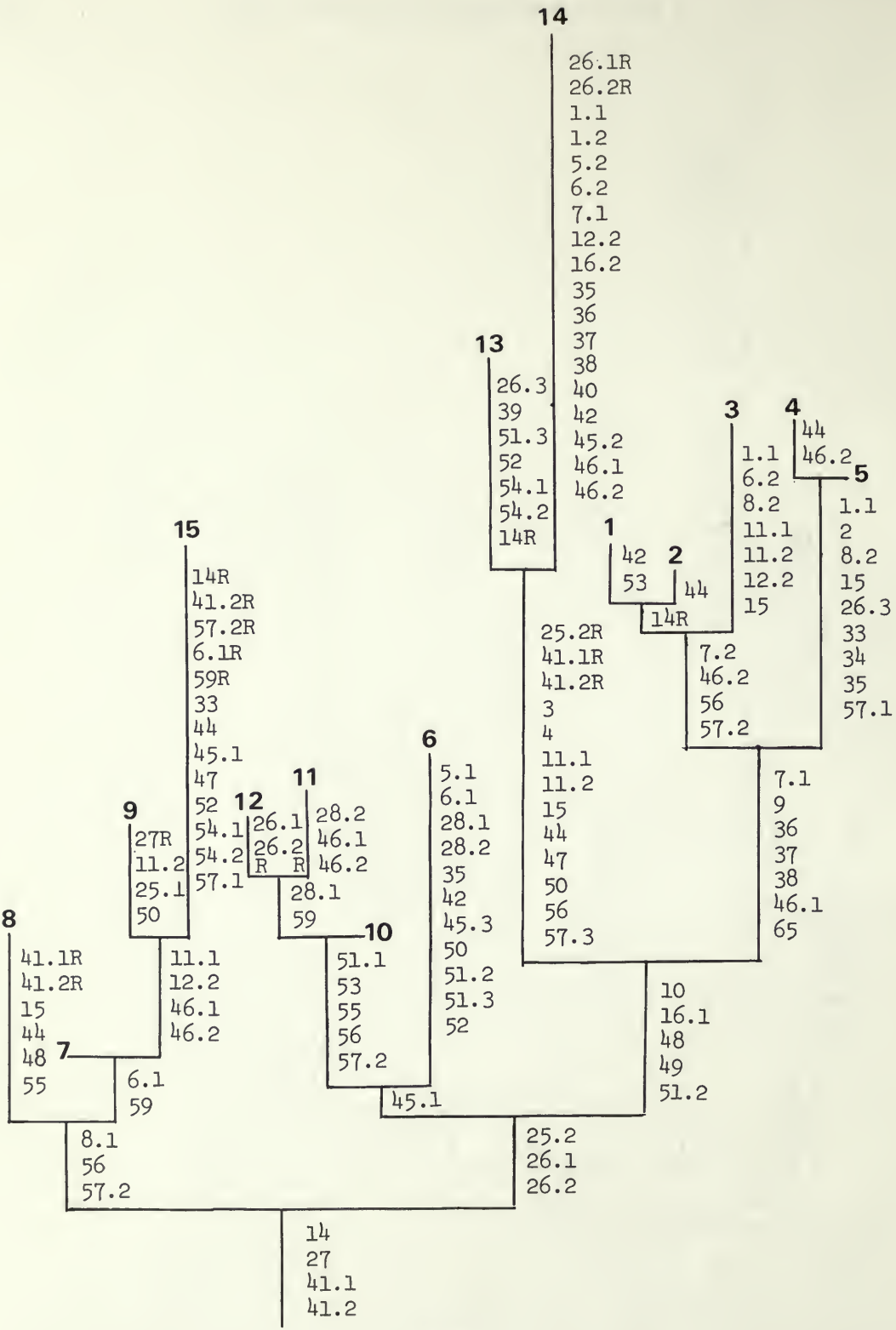

14
26.1R
26.2R
1.1
1.2
5.2
6.2
7.1
12.2
16.2
35
36
37
38
40
42
45.2
46.1
46.2
13
26.3
39
51.3
52
54.1
54.2
14R
3
1.1
6.2
8.2
11.1
11.2
12.2
15
4
44
46.2
5
1.1
2
8.2
15
26.3
33
34
35
57.1
1
42
53
2
44
14R
25.2R
41.1R
41.2R
3
4
11.1
11.2
15
44
47
50
56
57.3
7.2
46.2
56
57.2
7.1
9
36
37
38
46.1
65
15
14R
41.2R
57.2R
6.1R
59R
33
44
45.1
47
52
54.1
54.2
57.1
6
5.1
6.1
28.1
28.2
35
42
45.3
50
51.2
51.3
52
11
28.2
46.1
46.2
12
26.1
26.2
R R
28.1
59
9
27R
11.2
25.1
50
10
51.1
53
55
56
57.2
8
41.1R
41.2R
15
44
48
55
7
11.1
12.2
46.1
46.2
6.1
59
45.1
10
16.1
48
49
51.2
8.1
56
57.2
25.2
26.1
26.2
14
27
41.1
41.2

Fig. 5d

number of derived characters are added last. However Felsenstein (1981) recommends performing a number of runs, altering the order of input of taxa, as a trial & error strategy for finding the shortest tree.

In all four runs were undertaken:

1. Entire data set; advancement-index sequenced.
2. Entire data set; taxa in order of Le Quesne test labelling (see p. 156).
3. Characters with more arbitrarily scored polarities excluded; advancement-index sequenced.
4. Characters with more arbitrarily scored polarities excluded; Le Quesne test labelling governing the order of input of taxa (see p. 156).

With the full data set, examined by the unmodified sequence method (run 1), *Laticauda* and the true sea snakes appear not especially closely related; *Parapistocalamus* is sister to *Laticauda* (Fig. 5a). Altering the program to treat taxa in a modified order based on Le Quesne test labelling (run 2) produced a less parsimonious tree (213 steps vs. 204 steps). The topology of this tree (Fig. 5b) suggests that *Laticauda*, 'true' sea snakes and kraits *(Bungarus)* are all relatively closely related. Reducing the data set to consider only the more confidently scored characters (runs 3 and 4) produced two more topologies for consideration. In the advancement sequenced run (3) Fig. 5c, the tree was similar to that produced in run 1 in the sense that *Laticauda* and the true sea snakes appear only remotely related. However, run 3 estimates the sister of *Laticauda* to be not only *Parapistocalamus* but also *Micrurus*. Repeating the run, this time with Le Quesne test sequencing (run 4) Fig. 5d produced an equally parsimonious tree (the trees produced by both runs 3 and 4 are 139 steps). However, the topology of the tree resulting from run 4 resembles that of rejected run 2 in closely relating *Laticauda* and the 'true' sea snakes with each other, *Bungarus* is not considered close to the sea snakes though, instead *Parapistocalamus* and *Micrurus* together form the sea snake sister group.

Detection of homoplasies in Wagner trees

(i) Procedural estimate

The general amount of homoplasy (reversals and parallels) present in Wagner trees may be estimated by dividing the number of derived character states by the total number of character state changes (steps) in the tree. The result, expressed as a percentage, is termed the consistency ratio or homoplasy index. The homoplasy indices of various Wagner tree runs in the present study are as follows:

		Homoplasy Index
Run 1	89/204 × 100	43·63%
Run 2	89/213 × 100	41·78%
Runs 3 & 4	65/139 × 100	46·76%

In comparison, Kluge (1976: 45) derived a scheme for pygopodid lizards that has rather less 'noise' than is detected in the present study (its homoplasy index is 57·2%) whereas Moody's (1980: 124) Wagner tree for agamid lizards has almost twice as much homoplasy as the trees in the present study (the index is 24·7%).

The Wagner tree algorithm, by creating hypothetical intermediates at nodes, assesses the implications of each topology for every character state so that the number of reversals and parallels hypothesized for each character may be compared. Table 9 shows the changes of each character implicit in Wagner trees produced by runs 1, 3 and 4. However the Wagner tree algorithm gives a purely procedural estimate of homoplasies; some of the decisions, when judged by biological criteria, may appear unrealistic. For example, character 14 (vestigial left lung loss) is hypothesized to have been reversed three times in runs 3 and 4 but, biologically, a more likely explanation may be that such a vestige would have instead been lost, in parallel, on several occasions.

(ii) 'Fours' analysis

Underwood (1982) recently suggested a method for detecting parallelism. This program enables taxa to be selected in groups of four and gives the distribution of derived states among these taxa; in this way conflicts of evidence are clearly exposed.

Table 9. Number of parallels (P) & reversals (R) hypothesized for some Wagner tree runs.

Character	Run 4	Run 3	Run 1	Character	Run 4	Run 3	Run 1
1·1	2P	1P	2P	32	–	–	0
1·2	0	0	0	33	1P	1P	1P
2	0	0	0	34	0	0	0
3	0	0	0	35	2P	2P	2P
4	0	0	0	36	1P	1P	1P
5·1	0	0	0	37	1P	1P	1P
5·2	0	0	0	38	1P	1P	1P
6·1	1R, 1P	1P	1P	39	0	0	0
6·2	1P	1P	1P	40	0	0	0
7·1	1P	1P	1P	41·1	2R	1P	2R
7·2	0	1P	0	41·2	3R	0	1R
8·1	0	2R	1P	42	2P	2P	2P
8·2	1P	0	1P	43	–	–	1R, 4P
9	0	0	0	44	4P	3P	3P
10	0	1P	1P	45·1	1P	1P	2P
11·1	2P	2P	2P	45·2	0	0	0
11·2	2P	2P	2P	45·3	0	0	0
12·1	–	–	3P	46·1	3P	4P	4P
12·2	2P	3P	3P	46·2	4P	6P	5P
13	–	–	1R, 2P	47	1P	0	0
14	3R	1R, 1P	1R, 2P	48	1P	2P	2P
15	3P	2P	3P	49	0	1P	1P
16·1	0	1P	1P	50	2P	2P	2P
16·2	0	0	0	51·1	0	1R	0
17·1	–	–	1R	51·2	1P	2P	1P
17·2	–	–	0	51·3	1P	1P	1P
18	–	–	1R	52	2P	1R, 1P	1R, 1P
19	–	–	0	53	1P	1R, 1P	1P
20	–	–	2R, 1P	54·1	1P	1R	1R
21·1	–	–	0	54·2	1P	1R	1R
21·2	–	–	1R, 1P	55	1P	1R, 1P	1P
23·1	–	–	1R, 2P	56	3P	2R	2R
23·2	–	–	1P	57·1	1P	1P	1P
24	–	–	3P	57·2	1R, 2P	2R	1P
25·1	0	0	0	57·3	0	0	0
25·2	1R	0	1P	58	–	–	0
26·1	2R	2P	2P	59	1R, 1P	2P	2P
26·2	2R	2P	2P	60	–	–	2P
26·3	1P	1P	1P	61	–	–	2P
27	1R	1R	1R	62	–	–	2P
28·1	1P	1P	2P	63	–	–	1P
28·2	1P	0	1P	64·1	–	–	1P
29	–	–	2P	64·2	–	–	0
30	–	–	1R, 2P	65	0	0	0
31	–	–	0				

Seven species were selected to test the robustness of the various Wagner trees produced in the present study: *Laticauda crockeri, Laticauda semifasciata, Parapistocalamus hedigeri, Micrurus surinamensis, Ephalophis greyi, Aipysurus fuscus, Bungarus flaviceps.*

The topologies of these taxa in various Wagner tree runs are shown in Fig. 6. Table 10 gives an indication of the character states supporting various combinations of the seven species. Table

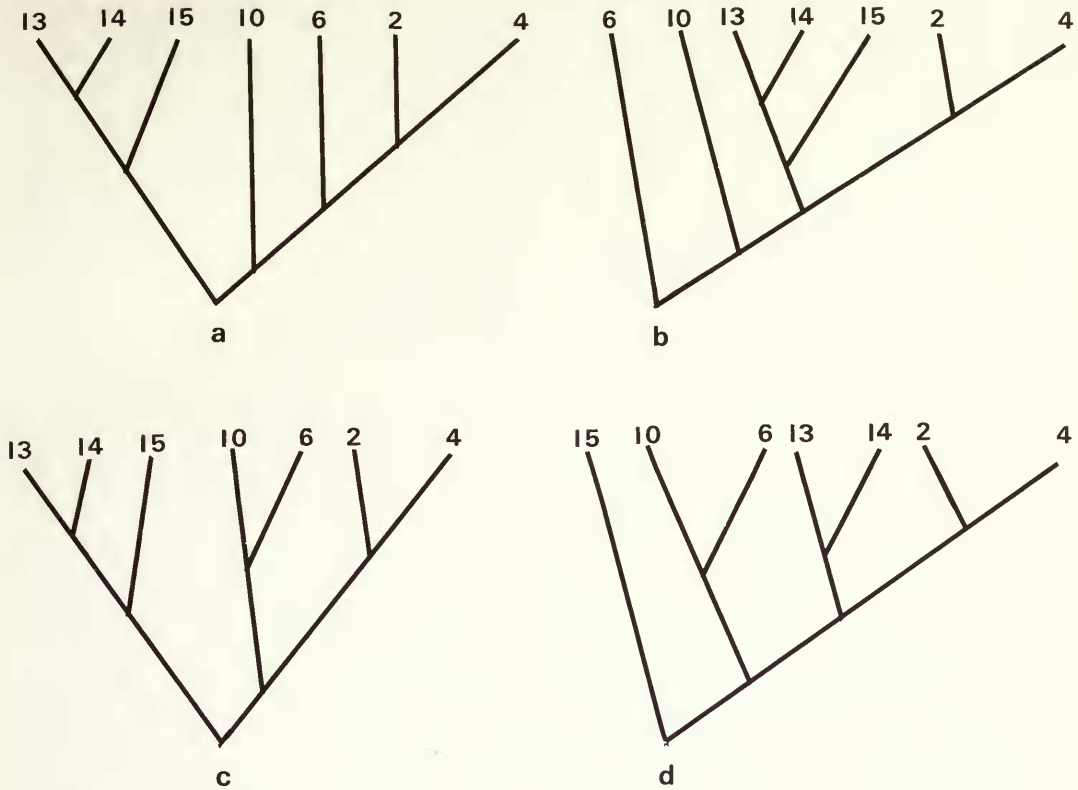


Fig. 6 'Fours' analysis. Topologies, in various Wagner tree runs, of seven taxa selected for 'fours' analysis. Taxa numbered as in Fig. 4. (a) Wagner tree run 1. (b) Wagner tree run 2. (c) Wagner tree run 3. (d) Wagner tree run 4.

10(a) deals with *Micrurus surinamensis* (10), *Parapistocalamus hedigeri* (6), *Laticauda crockeri* (2) and *Laticauda semifasciata* (4). Wagner run 1 suggests an asymmetric dichotomy pattern for these taxa whereas run 3 suggests symmetric dichotomies. Of the non-arbitrary characters supporting the alternatives there is a tie; one character 51·2 (saddle-joint between palatine and pterygoid) supporting run 1 while character 45·1 (position of the anterior vidian foramen) supports run 3. Three non-arbitrary characters are incompatible with either of these arrangements: 56 (parietal ridge) and 57·2 (prefrontal/frontal articulation) associate *Micrurus surinamensis* (10) and *Laticauda crockeri* (2), while 14 (absence of a vestigial left lung) occurs in *Micrurus* (10), *Parapistocalamus* (6) and *Laticauda semifasciata* (4). However the small number of characters suggesting that *L. crockeri* and *L. semifasciata* might have closer affinities with taxa outside the genus are outweighed by thirteen non-arbitrary derived characters shared by these two species of *Laticauda*.

Another fours print-out (Table 10b), this time replacing *Parapistocalamus* with *Aipysurus fuscus* (14) brings into consideration some of the characters supporting the affinities of *Laticauda* with other sea snakes. The proposition that *Micrurus surinamensis* (10) is more closely related to *Laticauda* (4) than is *Aipysurus* (14) (runs 1 and 3) is supported by five non-arbitrary characters but out-voted by twelve non-arbitrary characters supporting the close affinity of *Laticauda* with *Aipysurus*. Additionally, the assumption that *L. crockeri* is closely related to *L. semifasciata* (supported by characters 9 and 65) is challenged by three characters (1·1, 15 and 35) which suggest that *L. semifasciata* is more closely related to *Aipysurus*, a topology not suggested by any of the Wagner runs in the present study.

Table 10. 'Fours' analysis.

(*a*) Taxon numbers 10 6 2 4:-

1100:	–20 45·1
0011:	7·1 9 10 16·1 –19 36 37 38 44 46·1 46·2 48 49 65
1010:	–29 56 57·2
0101:	35
1101:	14
0111:	51·2
1000:	51·1 55
0100:	5·1 6·1 28·1 28·2 42 45·3 50 51·3 52
0010:	7·2
0001:	1·1 2 8·2 15 26·3 33 34 57·1

(*b*) Taxon numbers 10 2 4 14:-

1100:	–29 57·2
0011:	1·1 15 35
0101:	–12·1
1001:	–20 –21·2
0110:	9 –19 –23·1 –24 65
1110:	25·2 26·1 26·2 41·1 41·2
1101:	56
1011:	14
0111:	7·1 10 16·1 36 37 38 44 46·1 46·2 48 49 51·2
1000:	45·1 51·1 55
0100:	7·2
0010:	2 8·2 26·3 33 34 57·1
0001:	1·2 3 4 5·2 6·2 11·1 11·2 12·2 16·2 40 42 45·2 47 50 57·3

(*c*) Taxon numbers 10 13 4 14:-

0011:	1·1 7·1 35 36 37 38 46·1 46·2
1010:	–17·1 25·2 41·1 41·2 –62
0101:	3 4 11·1 11·2 –12·1 47 50 57·3
1001:	–20
0110:	26·3 –30
1110:	26·1 26·2
1101:	56
1011:	14
0111:	10 15 16·1 44 48 49 51·2
1000:	45·1 51·1 55 57·2
0100:	39 51·3 52 54·1 54·2
0010:	2 8·2 9 33 34 57·1 65
0001:	1·2 5·2 6·2 12·2 16·2 40 42 45·2

(*d*) Taxon numbers 10 15 4 14:-

1100:	45·1
0011:	1·1 7·1 10 –13 15 16·1 35 36 37 38 48 49 51·2
1010:	25·2 26·1 26·2 41·2 –62
0101:	11·1 –12·1 12·2 47
1001:	–20 –21·2
0110:	–24 –30 33 57·1
1110:	41·1
1101:	56
1011:	14
0111:	44 46·1 46·2
1000:	51·1 55 57·2
0100:	8·1 52 54·1 54·2
0010:	2 8·2 9 26·3 34 65
0001:	1·2 3 4 5·2 6·2 11·2 16·2 40 42 45·2 50 57·3

Character state numbers preceded by '–' are those for which polarity assessments are rather arbitrary. Arbitrary states are only given when these are shared between taxa.

Introducing another hydrophiine sea snake into the fours analysis and withdrawing *Laticauda crockeri* leads to the print-out given in Table 10 (c). Seven non-arbitrary characters support the inclusion of *Laticauda semifasciata* (4) in the same group as *Aipysurus* (14) and *Ephalophis* (13) whereas only three suggest that *L. semifasciata* is more closely related to *Micrurus surinamensis* (10) than it is to hydrophiine sea snakes. Relationships within the sea snakes are balanced between the seven non-arbitrary characters supporting the affinities of *Aipysurus* with *Ephalophis* and the eight non-arbitrary characters supporting the association of *Aipysurus* with *L. semifasciata.*

As *L. semifasciata* and *Aipysurus fuscus* are the respective laticaudines and hydrophiines that seem to have most derived characters in common, a fourth print-out (Table 10d) was obtained to assist in evaluating the evidence supporting laticaudine/hydrophiine relationships. In addition to *L. semifasciata* (4) and *A. fuscus* (14) the elapines *Bungarus flaviceps* (15) (a species which is associated with hydrophiine sea snakes in Wagner tree runs 1–3) and *Micrurus surinamensis* (10) are also included.

If it be assumed that *Laticauda* and hydrophiine sea snakes do not share close common ancestry it might be anticipated that the majority of derived features shared by the two groups would be parallel marine adaptations. However, of the twelve non-arbitrary derived states shared by *Laticauda semifasciata* and *Aipysurus fuscus,* only three appear to be likely aquatic adaptations, namely: 10 (paddle-shaped tail), 15 (tracheal lung present), 16 (muscular air sac). Of the other characters, 1·1 (azygous prefrontal) and 7·1 (marginal lower lip scales) are possibly not homologous in the two groups. *Aipysurus fuscus* is inclined to have its head shields irregularly fragmented therefore the inference that these are truly derived characters, shared by *Aipysurus* and *Laticauda*, may in fact be spurious. Absence of a palatine medial wing (49) and presence of a saddle-joint between palatine and pterygoid (51) are both found in a number of other taxa (Marx & Rabb, 1972 and McCarthy, 1982), and appear likely to have occurred independently several times in snake evolution. Broad flaring of the quadrato-maxillary ligament (35) has been found additionally in *Parapistocalamus.* The unusual hyoid muscle conditions in *Laticauda* and *Aipysurus* (characters 36, 37 and 38) do appear to be restricted to these two genera and may be potentially robust indicators of phyletic affinity but the extent of the distribution of these characters remains to be more fully investigated (McCarthy, in prep.). Character 48 (caudal haemapophyses fused) is unusual for snakes and might be a significant similarity shared between *Laticauda, Aipysurus, Emydocephalus,* and *Ephalophis;* the only elapines in which this state has been found are two species of *Calliophis* (McCarthy, 1982: 146).

Characters shared by *Laticauda semifasciata* and *Micrurus surinamensis* are:- venom gland down-turning (25·2), quadrate attachment of the superficialis muscle (26·1, 26·2) and a small dorsal extension of the dentary in comparison with the ventral extension (41·2). None of these characters are exclusively shared by *Laticauda* and *Micrurus* but at least 25·2 and 41·2 are rather restricted in their distributions among other elapids (McCarthy, 1982: 101 and 132). Characters 26·1 and 26·2 have rather wider distributions, occurring for example in a number of Australasian elapines (McDowell, 1967: 536 ff.).

Compatibility

In contrast to parsimony methods, which aim to find the shortest tree thereby minimizing assumptions of homoplasy, compatibility methods exist to find a tree which is compatible with the largest number of characters irrespective of the number of changes that may need to be assumed in other characters (Felsenstein, 1982). When pairs of binary characters are compared and all four possible combinations of states are found it is a logical consequence that at least one of the character states is not uniquely derived (Le Quesne, 1969).

The program used in the present study is that devised by Underwood, which compiles a character-pair matrix, works out the number of Le Quesne test incompatibilities per character and then computes the ratio between actual and expected failure rates. Additionally the number of times the occurrence of a character state in a particular species is uniquely responsible for Le Quesne test incompatibility is noted; this procedure is termed 'labelling' by Guise, Peacock & Gleaves (1982). The number of labelling events for each species is totalled (Table 11) and the

Table 11. Le Quesne test; the number of labelling events per taxon.

Taxon	Number of times labelled
1	86
2	50
3	156
4	10
5	6
6	125
7	19
8	85
9	56
10	17
11	37
12	19
13	98
14	203
15	111

results used to decide the order of input of taxa in some Wagner parsimony test runs (p. 151). This procedure for input of taxa may be desirable because initial construction of the Wagner tree can be accomplished using taxa with the fewest incompatibilities. 'Problem' taxa are later added to a relatively robust structure rather than being allowed to influence the topology of that structure at an early stage.

The Le Quesne test failure rates of the characters are shown in Table 12. An observed: expected ratio of 0·5 indicates those characters that have survived the test twice as well as could have been anticipated on a null hypothesis of random distribution of states of the characters (Le Quesne, 1972). Fourteen characters having a ratio of 0·5 or better are shown in Figure 7 together with the cladograms described by them. Ten of the fourteen characters that best survive the test can be nested within a single cladogram (Fig. 7a). These ten states suggest relationships within *Laticauda*, the distinctiveness of the genus and also its possible relationships with some hydrophiine sea snakes. Two character states (17·1 and 26·1) not entirely congruent with the arrangement suggest the relationships of *Laticauda* with particular groups of terrestrial elapines and one hydrophiine (Figs 7b & 7c). Two other character sites (55 and 59) suggest possible relationships between American and Asiatic elapines (Fig. 7d).

It may be concluded that those characters which best survive the Le Quesne test and which indicate the affinities of *Laticauda* with taxa outside the genus are:- 7·1 (marginal lower lip scales), 16·1 (muscular pulmonary air sac), 49 (absence of palatine medial wing). If Le Quesne's procedure is to be viewed as a weighting method (Arnold, 1981) these characters would be given relatively high weight in attempts to reconstruct a phylogeny of laticaudine sea snakes. Out of the various Wagner parsimony runs, run 4 (Fig. 5d) appears to be closest to the topology that would be preferred on the grounds of Le Quesne test results.

Conclusion

Following a study of the morphological evidence using most methods of analysis (some parsimony runs, 'fours', compatibility) it may be concluded that laticaudines and hydrophiines do indeed seem to be comparatively closely related. There is however still a residue of conflicting data which tend to support McDowell's contrasting proposition that *Laticauda* is more closely

Table 12. Le Quesne test: observed/expected failure rates.

Le Quesne's coefficient of character state randomness = Ratio × 100%
Failures: Observed expected ratio

1·1 : 54	57·59	0·94	1·2 : 2	0·67	2·99
2 : 3	31·85	0·09	3 : 29	39·93	0·73
4 : 29	39·93	0·73	5·1 : 4	1·69	2·37
5·2 : 27	10·73	2·52	6·1 : 35	47·33	0·74
6·2 : 43	37·21	1·16	7·1 : 25	52·98	0·47
7·2 : 16	45·82	0·35	8·1 : 31	46·65	0·66
8·2 : 38	47·23	0·8	9 : 29	56·13	0·52
10 : 21	54·09	0·39	11·1 : 49	55·75	0·88
11·2 : 47	50·51	0·93	12·1 : 23	41·86	0·55
12·2 : 52	51·57	1·01	13 : 37	56·32	0·66
14 : 46	54·39	0·85	15 : 30	52·48	0·57
16·1 : 27	56·19	0·48	16·2 : 3	1·06	2·83
17·1 : 13	24·01	0·54	17·2 : 0	–	–
18 : 27	33·7	0·8	19 : 30	55·32	0·54
20 : 36	51·85	0·69	21·1 : 3	30·8	0·1
21·2 : 36	54·49	0·66	23·1 : 33	54·58	0·6
23·2 : 33	28·19	1·17	24 : 37	57·93	0·64
25·1 : 0	–	–	25·2 : 27	51·93	0·52
26·1 : 24	48·64	0·49	26·2 : 31	49·41	0·63
26·3 : 26	41·32	0·63	27 : 0	14·61	0
28·1 : 25	39·24	0·64	28·2 : 22	26·3	0·84
29 : 48	58·97	0·81	30 : 34	50·01	0·68
31 : 24	39·22	0·61	32 : 26	41·8	0·62
33 : 21	40·53	0·52	34 : 3	31·33	0·1
35 : 36	49·32	0·73	36 : 34	59·8	0·57
37 : 34	59·8	0·57	38 : 36	60	0·6
39 : 0	–	–	40 : 3	1·06	2·83
41·1 : 39	47·48	0·82	41·2 : 41	52·03	0·79
42 : 48	39·13	1·23	43 : 40	47·57	0·84
44 : 64	63·28	1·01	45·1 : 27	49·83	0·54
45·2 : 3	1·06	2·83	45·3 : 0	–	–
46·1 : 42	58·72	0·72	46·2 : 56	59·58	0·94
47 : 27	30·62	0·88	48 : 63	66·65	0·95
49 : 29	59·7	0·49	50 : 33	41·39	0·8
51·1 : 4	40·32	0·1	51·2 : 44	61·92	0·71
51·3 : 10	12·09	0·83	52 : 21	26·39	0·8
53 : 37	45·26	0·82	54·1 : 5	11·86	0·42
54·2 : 6	12·36	0·49	55 : 22	49·95	0·44
56 : 48	52·63	0·91	57·1 : 26	41·59	0·63
57·2 : 47	63·58	0·74	57·3 : 21	23·82	0·88
58 : 39	50·5	0·77	59 : 20	49·94	0·4
60 : 56	52·9	1·06	61 : 31	50·62	0·61
62 : 54	64·87	0·83	63 : 57	47·87	1·19
64·1 : 27	24·7	1·09	64·2 : 38	38·82	0·98
65 : 25	60·89	0·41			

Grand total
Failures: Observed expected ratio

1276	1822·01	0·7

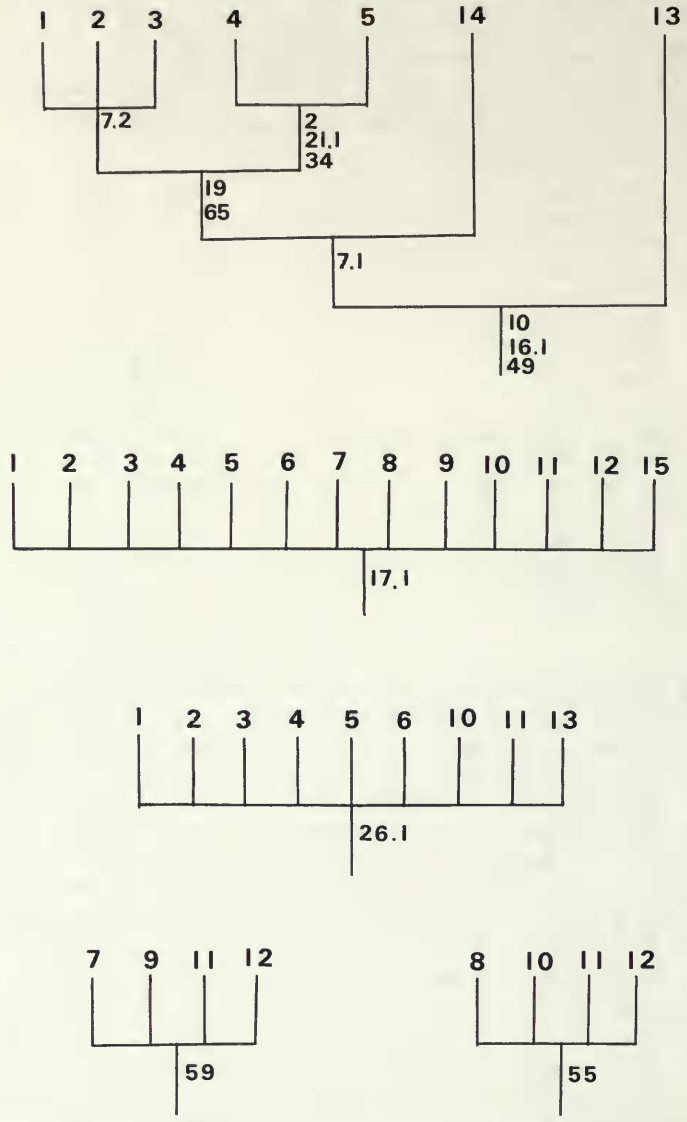


Fig. 7 Le Quesne test cladograms, described by characters having an observed: expected survival ratio $<0{\cdot}5$.

related to particular groups of terrestrial elapines than to hydrophiines (a topology suggested both by phenetic analysis and by some parsimony runs).

Evidence from immunology (e.g. Cadle & Gorman, 1981; Mao *et al.*, 1983) and karyology (Mengden pers. comm.) again indicates that the affinities of laticaudines lie with hydrophiines (and Australian terrestrial elapids) although samples tested so far appear not to have included some taxa which McDowell hypothesises to be closely related to *Laticauda* i.e. *Calliophis, Maticora* and *Parapistocalamus.*

The method of sample selection in the present study (Table 4) has led to the terrestrial sample to be rather biased towards Asiatic and American elapids. Given some of the recent evidence provided by biochemical and chromosomal data it would be instructive for future studies further

to investigate Australian terrestrial elapids to assess the degree to which the apparent affinity of this group with laticaudines and hydrophiines is corroborated by morphological evidence.

The present assessment of the relationships of laticaudine sea snakes must therefore be that, while the bulk of the evidence examined supports the affinity of laticaudines with hydrophiines, more information is required about the distribution of some characters in order to be able to resolve precisely the relationships of either sea snake group with particular groups within the largely terrestrial Elapinae. The classification recommended by McCarthy (1985) with Elapinae, Laticaudinae and Hydrophiinae treated as equivalent subfamilies of the Elapidae reflects the present lack of clear resolution in the relationships between the three subfamilies, a situation that hopefully will be improved as more morphological, biochemical and karyological information becomes available.

Acknowledgements

This paper is mainly derived from a Council for National Academic Awards post-graduate research project that was supervised by Dr G. Underwood (City of London Polytechnic) and Miss A. G. C. Grandison (British Museum (Natural History)); Dr A. L. Panchen (University of Newcastle) was the external examiner. I am very grateful to these people for their guidance and am particularly indebted to Dr Underwood for supplying the computer programs. The work was mainly conducted at the British Museum (Natural History) and I am especially grateful to the following colleagues for their interest and advice: Dr E. N. Arnold (who also kindly read an earlier draft of the paper), Dr J. G. Sheals, Mr J. F. Peake, Mr B. T. Clarke, Mr A. F. Stimson, Mr J. C. M. Dring, and Dr B. C. Groombridge. The following workers generously informed me about their activities: Dr J. Cadle (University of California), Dr H. Cogger (Australian Museum), Mr M. Guinea (Northern Territory, Australia), Dr G. Mengden (Australian Museum), Dr J. Villa (University of Missouri), Dr H. Voris (Field Museum, Chicago). Professor L. D. Brongersma (Leiden) very kindly arranged a travel grant from the 'Zoologisch Insulinde Fonds' which facilitated the study of *Laticauda* specimens in the Rijksmuseum van Natuurlijke Historie (Leiden) and the Zoologisk Museum (Copenhagen). Dr M. S. Hoogmoed (Leiden) thoughtfully drew my attention to an unpublished manuscript by Mr H. Enderman, which deals with the subject of geographical variation in sea snakes. My gratitude also goes to the following curators for arranging loans of useful material in their care: Dr W. Auffenberg (University of Florida), Dr H. Cogger (Australian Museum), Dr R. C. Drewes (California Academy of Sciences), Dr J. B. Rasmussen (Zoologisk Museum, Copenhagen), Dr E. E. Williams (Museum of Comparative Zoology, Harvard), Dr H. Voris (Field Museum of Natural History, Chicago), Dr G. Zug (Smithsonian Institution, Washington D.C.).

References

Alvarez del Toro, M. 1982. *Los reptiles de Chiapas* (3rd Edition). Chiapas.

Anderson, J. 1871. On some Indian Reptiles. *Proceedings of the Zoological Society of London.* **1871:** 149–211.

Arnold, E. N. 1981. Estimating phylogenies at low taxonomic levels. *Zeitschrift fur Zoologische Systematik und Evolutionsforschung.* Frankfurt. **19** (1): 1–35.

Boulenger, G. A. 1896. *Catalogue of the snakes in the British Museum (Natural History)* **3.** London.

Cadle, J. E. & Gorman, G. C. 1981. Albumin immunological evidence and the relationships of sea snakes. *Journal of Herpetology* **15** (3): 329–334.

Cogger, H. G. 1975. Sea snakes of Australia and New Guinea. *In* W.A. Dunson, *The Biology of Sea Snakes*: 59–139. Baltimore, London and Tokyo.

Dowling, H. G. & Duellman, W. E. 1978. Systematic Herpetology: A synopsis of families and higher categories. *Publications in Herpetology,* New York. **7.**

Enderman, H. 1970. *A classification of the sea snakes with notes on geographic variation.* Rijksmuseum van Natuurlijke Historie, Leiden (unpublished ms.).

Felsenstein, J. 1981. *Package for inferring phylogenies* (Version 2·0). University of Washington.

—— 1982. Numerical methods for inferring evolutionary trees. *The Quarterly Review of Biology.* **57** (4): 379–404.

Gorman, G. C. 1981. The chromosomes of *Laticauda* and a review of karyotype evolution in the Elapidae. *Journal of Herpetology* **15** (2): 225–233.

Guinea, M. L. 1981. The sea snakes of Fiji. *Proceedings of the Fourth International Coral Reef Symposium*, Manila **2:** 581–585.

——, **Tamiya, N. & Cogger, H. G.** 1983. The neurotoxins of the sea snake *Laticauda schistorhynchus*. *Biochemical Journal* **213:** 39–41.

Guise, A., Peacock, D. & Gleaves, T. 1982. A method for identification of parallelism in discrete character sets. *Zoological Journal of the Linnean Society* London **74** (3): 293–303.

Kharin, V. E. 1984. Revision of sea snakes of the subfamily Laticaudinae Cope, 1879 Sensu Lato (Serpentes, Hydrophiidae). *In* L.J. Borkin (Ed.) Ecology and Faunistics of Amphibians and Reptiles of the USSR and adjacent countries. *Proceedings of the Zoological Institute, Leningrad.* **124:** 128–139.

Klemmer, K. 1963. Liste der rezenten Giftschlangen. Elapidae, Hydropheidae, Viperidae und Crotalidae. *In* Behringwerk-Mitteilungen, *Die Giftschlangen der Erde*: 255–464. Marburg/Lahn.

Kluge, A. G. 1976. Phylogenetic relationships in the lizard family Pygopodidae: an evaluation of theory, methods and data. *Miscellaneous Publications of the Museum of Zoology, University of Michigan.* **152:** 1–72.

Le Quesne, W. J. 1969. A method of selection of characters in numerical taxonomy. *Systematic Zoology* **18:** 201–205.

—— 1972. Further studies based on the uniquely derived character concept. *Systematic Zoology* **21**: 281–288.

Linnaeus, C. 1758. *Systema Naturae* (10th Edition), **1**. London (Photographic facsimile 1956).

Mao, S.-H. & Chen, B.-Y. 1980. *Sea snakes of Taiwan.* National Science Council, Taipei. Special Publication **4:** xi + 1–62 pp.

——, **Chen, B.-Y., Yin, F.-Y. & Guo, Y.-W.** 1983. Immunotaxonomic relationships of sea snakes to terrestrial elapids. *Comparative Biochemistry and Physiology* **74A** (4): 869–872.

Marx, H. & Rabb, G. B. 1972. Phyletic analysis of fifty characters of advanced snakes. *Fieldiana, Zoology.* Chicago. **63:** viii + 321 pp.

McCarthy, C. J. 1982. *Relationships of the laticaudine sea snakes.* Ph.D. thesis. Council for National Academic Awards (City of London Polytechnic).

—— 1985. Monophyly of elapid snakes (Serpentes: Elapidae). An assessment of the evidence. *Zoological Journal of the Linnean Society,* London. **83:** 79–93.

—— (in preparation). Adaptations of sea snakes that eat fish eggs.

McCoy, M. 1980. *Reptiles of the Solomon Islands.* Wau Ecology Institute Handbook **7:** vi, 1–80 + 20 Pls.

McDowell, S. B. 1967. *Aspidomorphus,* a genus of New Guinea snakes of the family Elapidae, with notes on related genera. *Journal of Zoology,* London. **151:** 497–543.

—— 1969. Notes on the Australian sea snake *Ephalophis greyi* M. Smith (Serpentes: Elapidae, Hydrophiinae) and the origin and classification of sea snakes. *Zoological Journal of the Linnean Society,* London **48:** 333–349.

—— 1972. The genera of sea-snakes of the *Hydrophis* group (Serpentes: Elapidae). *Transactions of the Zoological Society of London* **32:** 189–247.

—— 1974. Additional notes on the rare and primitive sea-snake, *Ephalophis greyi. Journal of Herpetology* **8** (2): 123–128.

Moody, S. M. 1980. *Phylogenetic and historical biogeographical relationships of the genera in the family Agamidae (Reptilia, Lacertilia).* Doctoral Thesis (University of Michigan).

Schlegel, H. 1837. *Essai sur la physionomie des Serpens* (vol. 2). La Haye.

Schneider, J. G. 1799. *Historia Amphibiorum naturalis et literariae* (Fasciculus Primus). Facsimile Edition, Amsterdam.

Slevin, J. R. 1934. The Templeton Crocker Expedition to Western Polynesian and Melanesian Islands, 1933. No. 15. Notes on the Reptiles and Amphibians, with the description of a new species of sea-snake. *Proceedings of the California Academy of Sciences.* Fourth Series. **21** (15): 183–188.

Smith, H. M., Smith, R. B. & Sawin, H. L. 1977. A summary of snake classification. *Journal of Herpetology* **11** (2): 115–121.

Smith, M. A. 1926. *Monograph of the sea-snakes (Hydrophiidae).* London.

—— 1943. *The fauna of British India, Ceylon and Burma including the whole of the Indo-Chinese sub-region.* Reptilia and Amphibia. Vol. 3—Serpentes. London.

Sneath, P. H. A. & Sokal, R. R. 1973. *Numerical Taxonomy.* San Francisco.

Stejneger, L. 1907. Herpetology of Japan and adjacent territory. *Bulletin of the United States National Museum.* Washington D.C. **58:** xvii + 577 pp.

Tamiya, N., Sato, A., Kim, H. S., Teruuchi, T., Takasaki, C., Ishikawa, Y., Guinea, M. L., McCoy, M., Heatwole, H. & Cogger, H. G., 1983. Neurotoxins of sea snake genus *Laticauda. Toxicon* Suppl. **3:** 445–447.

Underwood, G. 1967. *A contribution to the classification of snakes*. British Museum (Natural History) Publication **653.** London.

—— 1982. Parallel evolution in the context of character analysis. *Zoological Journal of the Linnean Society*. London. **74** (3): 245–266.

Villa, J. 1962. *Las serpientes venosas de Nicaragua*. Managua, [only pp. 30–31 seen].

Volsøe, H. 1956. Herpetology of Rennell Island. *Natural History of Rennell Island, British Solomon Islands* **1** (8): 121–134.

—— 1958. Additional specimens of snakes from Rennell Island. *Natural History of Rennell Island, British Solomon Islands* **1** (12): 227–228.

Voris, H. K. 1969. *The evolution of the Hydrophiidae with a critique on methods of approach*. Ph.D. thesis, University of Chicago, [only pp. 368–369 seen].

—— 1977. A phylogeny of the sea snakes (Hydrophiidae). *Fieldiana, Zoology*. Chicago **70** (4): 79–169.

Wolff, T. 1969. The fauna of Rennell and Bellona, Solomon Islands. *Philosophical Transactions of the Royal Society of London. B* **255:** 321–343.

—— 1970. Lake Tegano on Rennell Island, the former lagoon of a raised atoll. *Natural History of Rennell Island, British Solomon Islands*. **6** (61): 7–29.

Manuscript accepted for publication 21 October 1985